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OF

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The relation of humidity and temperature to the development of three species of African locusts—*Locusta migratoria migratorioides* (R. & F.), *Schistocerca gregaria* (Forsk.), *Nomadacris septemfasciata* (Serv.). By ANDREW G. HAMILTON, B.Sc., B.Agr., Ph.D., D.I.C. . . . . pp. 1–60, pls. 1–2

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TRANSACTIONS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF LONDON

VOL. 85. 1936.

THE RELATION OF HUMIDITY AND TEMPERATURE TO THE DEVELOPMENT OF THREE SPECIES OF AFRICAN LOCUSTS—*LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. & F.), *SCHISTOCERCA GREGARIA* (FORSK.), *NOMADACRIS SEPTEMFASCIATA* (SERV.)

By ANDREW G. HAMILTON, B.Sc., B.Agr., Ph.D., D.I.C.,

(Assistant Entomologist, Imperial Institute of Entomology.)

[Read 20th November, 1935.]

WITH TWO PLATES AND TWENTY-SIX TEXT-FIGURES.

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I. Introduction.

The work described in this paper was carried out at the Locust Laboratory of the Imperial Institute of Entomology, British Museum (Natural History), London, and at the Royal College of Science.

The experiments were designed to determine the factors which influence the life-cycle of locusts in the different climates to which they are subjected in nature. Particular attention was given to the effect of humidity and temperature on sexual maturation and to the possibility of development without the intervention of a diapause.

The material for raising stocks of locusts for experimental purposes was obtained as follows :—

1. *Locusta migratoria migratorioides* R. & F. :—Anglo-Egyptian Sudan and Kenya.

2. *Schistocerca gregaria* Forsk. :—Morocco and Egypt.

3. *Nomadacris septemfasciata* Serv. :—Northern Rhodesia and Tanganyika Territory.

All the experiments were carried out using locusts of the transient phase; no attempt was made to produce either the solitary or gregarious phases.

Most of the experiments were carried out in glass tanks (15 inches × 15 inches and 20 inches high), fitted with suitable lids (pl. 1). The cages, with the exception of those run under room conditions, were heated with electric heaters controlled by a thermostat which could be regulated for temperatures between 75° F. and 110° F. Light was supplied by a 40-watt vacuum bulb hanging in the centre of the cage and only switched on for approximately 8 hours during the day.

For ordinary breeding the floor of the cages was covered with sand to a depth of 3–4 inches (cage as in pl. 1 without zinc floor). In order to prevent the sand becoming sodden it was found advisable to place pieces of broken earthenware below it. The females oviposited in this sand. In the experimental cages the hoppers were kept under the same conditions as those described for breeding, but the cages containing adults had an additional floor of perforated zinc raised 4 to 4½ inches. Glass tubes (4 inches × 1 inch or 4½ inches × 1½ inches) filled with moist sand were inserted through holes cut in the zinc so that the top edge was level with the zinc. The locusts oviposited in these tubes which were examined daily for egg-pods, so that it was possible to determine, approximately, when the eggs were deposited. All sand was sterilised by baking for several hours before being moistened and used.

Throughout this paper humidities are given in terms of relative humidity, and not as saturation deficiency, which has been used by many recent workers, because it was found that saturation deficiency did not explain the reactions of hoppers or adults to air with different moisture content. This is shown by the following results obtained in experiments on *Schistocerca* hoppers :—at 80° F. (26·7° C.) and 25% relative humidity (Saturation deficiency ·775) it was impossible for development to take place, but at 80° F. and 35% relative humidity (Saturation deficiency ·672) a few individuals succeeded in reaching the adult stage. At 90° F. (32·2° C.) and 35% relative humidity (Saturation deficiency ·925) all died during the hopper stages, but at 90° F. and 45% relative humidity (Saturation deficiency ·783) development occurred. Likewise at 100° F. (37·8° C.) and 35% relative humidity (Saturation deficiency 1·259) the hoppers were unable to complete development, but at 100° F. and 45% relative humidity (Saturation deficiency 1·065) a few reached the adult stage, but not so high a percentage as at 90° F. and 45% relative humidity. This shows that at practically the same saturation deficiencies, viz. ·775 and ·783, but at the temperatures of 80° F. and 90° F. respectively, entirely different results are obtained. As the humidities are increased above those mentioned there is a gradual rise in the percentage of hoppers becoming adult until the optimum condition is reached, when the percentage decreases again as will be seen later in the paper. This decrease is not marked until relative humidities of 80% and over are reached. At 80° F. and 85% relative humidity (Saturation deficiency ·155) it was possible for development to take place and adults emerged in 32–34 days. With an increase in temperature to 90° F. and at 85% relative

humidity (Saturation deficiency ·213) development was greatly retarded and no individuals succeeded in reaching the adult stage. Likewise at 90° F. and 80% relative humidity (Saturation deficiency ·284) development was slow and the adult stage was not reached, while at 90° F. and 75% relative humidity (Saturation deficiency ·356) development required very little longer time than under optimum conditions. At 100° F. as at 90° F. hoppers failed to reach the adult stage at 80% relative humidity (Saturation deficiency ·388) and 85% relative humidity (Saturation deficiency ·231). This shows that at 80° F. it is possible for hoppers to complete development at saturation deficiency between ·672 and ·155, at 90°F. between ·783 and ·284 and at 100° F. between 1·065 and ·571 (possibly much less).

From this data it is obvious that results cannot be given in terms of saturation deficiency without recording the temperature. One point worthy of note is that at high humidities it is possible to reduce saturation deficiency to a lower figure at 80° F. than at 90° F. and lower at 90° F. than at 100° F. and still obtain development, which is rather different from what might be expected.

The humidity was generally controlled to within ± 5%, but in many cases the variation was not more than 2%. Relative humidities above 45% were produced by adding varying quantities of water to the sand in the cage according to the humidity required. Humidities below 45% were obtained by suspending wire gauze containers filled with silica gel (SiO_2) in the cage, part of the silica gel having been previously treated with cobalt nitrate ($Co(NO_3)_2$) which acted as an indicator. Silica gel treated in this way is blue when dry but gradually changes to pink as moisture is absorbed. When the silica gel had taken up all the moisture it was capable of absorbing, at the required humidity, it was removed and heated for 2 hours at a temperature of 300° F. (149° C.) to 340° F. (171° C.), which dried out the moisture and enabled it to be utilised again.

Edney Paper hygrometers and a Humatagraph were used for estimating the humidity in the cages. It was found that more satisfactory results were obtained from these hygrometers if used over a small variation in humidity and standardised within the required range. Jars containing sulphuric acid (H_2SO_4) of known concentration at a known temperature were employed for standardisation (Wilson 1921).

As food, grass or young wheat was supplied daily to each cage. Occasionally bamboo (*Arundinaria japonica*), banana leaves and papyrus grass (*Cyperus papyrus* L.) were added. *Schistocerca gregaria* was also supplied with *Polygonum cuspidatum* S. & Z.

Hoppers were given freshly cut food but that supplied to the adults, both in high and low humidity cages, was partially dried with hot air in a fume "cupboard." This made it possible to maintain the low humidity cages at a much more constant humidity and as all were given food of approximately the same water content no variation in fertility, etc., could result from the food. Care was taken when drying the food that only the external moisture was removed, so that practically all the sap was retained. The water content of the partially dried grass and wheat was estimated and found to be on the average 38% and 37% respectively.

II. General Life-Cycle.

A very brief account of the life-cycle of the three species as known in Africa is given here.

(*a*) African migratory locust *Locusta migratoria migratorioides* (R. & F.).

It is now known definitely that there are usually two generations of this species in a year (Lean 1931; Uvarov 1933; Zolotarevsky 1933), except in Northern Rhodesia where it has been shown by Allan (1932) and Uvarov (1934) that there is generally only one generation a year; in this case there is an adult diapause of approximately eight months. Occasionally, however, some of the first individuals to reach the adult stage become sexually mature and oviposit thus giving a partial second generation which becomes mixed with the first.

Although the species may be found where the humidity is low, swarms on the whole remain where the relative humidity is between 40 and 85% (Lean 1931*a*). This humidity corresponds to that of the areas of the three main types of vegetation, viz. "High grass-low tree savanna," "acacia-tall grass savanna" and "acacia-desert grass savanna." Lean has further shown that breeding only takes place where the humidity is between 60 and 80%.

The time required to attain sexual maturity under natural conditions varies between 12 days (Johnston and Maxwell-Darling 1931) and 11 to 15 weeks (Lean 1931*a*). Eggs are deposited in either light or heavy soil and the incubation period takes from 11 to 25 days (Johnston and Maxwell-Darling 1931), dependent on the time of year. The number of hopper stages is generally five and this number has been described by Uvarov (1928) and Johnston and Maxwell-Darling (1931), but, on the other hand, Zolotarevsky (1933) found that all the females and the majority of the males of the Madagascan subspecies *Locusta migratoria capito* Sauss., bred in open air cages in the breeding area, passed through six hopper stages.

(*b*) Desert Locust *Schistocerca gregaria* (Forsk.).

This species is found in a much drier range of conditions than those required by the African Migratory Locust. Uvarov (1933*a*) has shown that the seasonal cycle of swarms of this species is fairly constant. He described the annual cycle as follows:—"The swarms bred in the Mediterranean countries in the spring, undoubtedly migrate southwards across the Sahara until they encounter the summer-rain zone in about July and August. Eggs are then laid in suitable localities and the resulting swarms reach the adult stage in September and October. These swarms then begin a northward migration, reaching the mountains bordering the Sahara on the north by the end of the year. The invasion of the Mediterranean countries continues throughout the early months of the following year, until the climate conditions become sufficiently favourable for egg-laying. Thus, the normal annual cycle consists of two generations, one breeding in the spring in the Mediterranean region, and the other breeding during the summer rains immediately south of the Sahara. As might be expected, the instability of the annual weather cycle in the Sahara and in the adjoining countries often affects the general scheme of generations outlined above. A failure, for example, of the summer rains in the usual summer-breeding area south of the Sahara may result either in the dying out of the swarms which had arrived there from the north; or in their surviving without reaching sexual maturity, in which case they return northwards again. In the latter event, only one generation in a year would be produced. There are reasons for believing that this does occasionally happen."

In North-eastern Kordofan (Anglo–Egyptian Sudan), where this species occurs in the solitary phase, Maxwell-Darling (1934) found that there is only one generation a year which breeds during the rainy season (July–September).

Likewise, Zolotarevsky, de Lépiney and Dupont (1934) record a single generation a year in the French Sudan. This shows that the time required to become sexually mature is regulated by the rains. This species prefers moist sandy soil for oviposition and the incubation period varies from an average of 32 days in the spring to 87 days during the winter (Ballard, Mistikawi and Zoheiry 1932), the minimum period being given as 14 days.

There are usually five hopper stages (Uvarov 1928) but occasionally there are six in females (Ballard, Mistikawi and Zoheiry 1932); the length of hopper life being approximately one month.

(*c*) Red Locust *Nomadacris septemfasciata* (Serv.).

The annual life-cycle of this species, unlike that of the other two, is characterised by a single breeding period coinciding with the rainy season which, in the areas invaded by it, generally occurs from December to April (Uvarov 1933*a*). Approximately nine months of the year are spent in the adult stage. After the commencement of the dry period in Northern Rhodesia the young swarms migrate gradually north and north-westwards, where they remain for a considerable time before starting on a return migration in the reverse direction. This return migration coincides with the beginning of the rainy season in the south where the locusts return to breed. The exact distance of either the north or south migrations appears to be controlled to a certain extent by the climatic conditions encountered by the swarms.

A few days after general mating the eggs are deposited in most types of soil, the only essential condition appears to be that of softness (Mossop 1933, 1933*a*). The incubation period varies very considerably with temperature, lasting from 14 to 54 days (Uvarov 1933*a*; Mossop 1933*a*). It was formerly thought that this species passed through five larval stages, but now six stages seem to be the recognised number, the latter number has been described by Mossop (1933*a*; also Michelmore and Allan, 1934). The complete hopper development takes from eight to eleven weeks (Mossop 1933*a*).

III. The Effect of Constant Humidity and Constant Temperature on Hopper Development.

(a) *Humidity.*

The moisture content of the air plays an important part in the development of the hoppers of all three species.

It may be seen (Table 1) that for *Locusta* relative humidities between 50% and 75% are suitable for development and that at lower or higher humidities there is a marked decrease in development and a smaller percentage of hoppers reach the adult stage. It should be pointed out that within this suitable range of relative humidities there is an optimum relative humidity which varies slightly with temperature, as does also the lower and upper limits of humidity which inhibit development.

Experiments at 80° F. (26·7° C.) have only been carried out on *Locusta* at relative humidities ranging from 25% to 85%. It may be seen from Table 1 that hoppers fail to develop at 25% relative humidity but succeed at 35% and at all relative humidities between this and 85%. The variation in the length of hopper life at the different relative humidities is so great that it is not possible to state definitely at what relative humidity optimum development takes place. As experiments were not conducted at relative humidities above 85% at this temperature it is difficult to say what relative humidity will inhibit development.

I consider development unlikely to occur at relative humidities much higher than 85%, because at this figure only 11·1% of the hoppers reached the adult stage.

Table 1.

Locusta migratoria migratorioides.

Table showing the effect of humidity and temperature on the rate of hopper development and the percentage of hoppers becoming adult.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of hoppers.	Length of hopper life.						No. of hoppers becoming adult.		% of hoppers becoming adult.
					Average.		Min.		Max.				
					♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	
26	22.v.35	80° F. (26·7° C.)	25	52	—	—	—	—	—	—	All dead by 7th day.		
25	4.iii.35		35	86	31·1	32·0	29	30	33	33	14	8	25·6
29	22.viii.34		70	32	39·5	42·7	31	40	47	45	16	3	59·4
23	27.ii.35		75	140	41·5	38·4	33	33	48	46	35	36	50·7
9	11.xi.35												
J1	9.xii.33		80	186	56·4	56·4	42	49	60	68	23	32	29·5
6	25.iv.34												
22	30.iv.35		85	100	49·0	48·2	42	42	52	56	4	6	11·1
B.S	2.v.35	90° F. (32·2° C.)	25	27	—	—	—	—	—	—	All dead by 23rd day.		
19	8.iv.35		35	50	27·7	31·3	24	28	30	34	6	6	24·0
J.A	19.ii.34		45	32	32·0	32·5	30	29	35	40	3	11	43·7
24	8.x.34		55	20	29·4	31·5	24	28	34	35	10	4	70·0
17	16.ii.35		60	63	26·4	28·8	24	26	32	32	23	21	69·8
17	27.v.34		65	71	27·5	28·2	22	26	33	35	30	25	77·5
19	5.ix.34												
16	1.xii.34		70	78	27·3	28·3	22	22	31	36	39	26	83·3
17	23.vi.35												
20	4.iv.34		75	87	31·6	30·6	25	27	43	38	35	21	64·3
8	21.v.34												
3J	12.iii.34		80	73	32·6	33·4	30	30	33	35	13	13	35·6
14	8.vii.35												
18J	2.xii.34		85	129	38·2	38·6	36	36	43	43	5	10	11·6
21	3.xii.34												
B.J	7.v.35		95	35	—	—	—	—	—	—	All dead by 5th day.		
12	9.xi.34	100° F. (37·8° C.)	35	51	—	—	—	—	—	—	All dead by 4th day.		
12	10.xii.34		45	57	29·7	29·7	25	29	34	30	3	3	10·5
3	9.ix.34		60	13	22·0	26·2	22	23	22	28	2	6	61·5
21	21.viii.34		65	16	22·0	26·6	20	23	24	31	4	8	75·0
12	2.x.34		70	68	24·4	25·7	20	20	30	30	20	20	61·8
4	19.x.33												
11	20.viii.35												
1	12.iv.34		75	100	30·0	32·2	24	24	38	40	27	24	51·0
27	10.ix.35		85	53	30·8	28·8	26	26	35	35	13	10	43·4
11J	10.v.35		95	13	—	—	—	—	—	—	All dead by 7th day.		
8	7.xi.33	110° F. (43·3° C.)	65	39	20·4	21·2	18	19	24	23	9	10	48·7

Experiments at 90° F. (32·2° C.) have been conducted at relative humidities below and above those at which the hoppers were able to complete their development. It was found that hoppers fail to develop at 25% relative humidity but succeed at 35%, which is similar to the results obtained at 80° F. As the relative humidity is increased there is an increase in the rate of development until, between 60% and 70%, there is a definite optimum. At a greater relative humidity than 70% the rate of development decreases until, at 95%, hoppers fail to reach the adult stage.

At 100° F. (37·8° C.) experiments have also been conducted at relative humidities below and above those at which complete development takes place. In this case it was not necessary to investigate the effect of relative humidity below 35% as hoppers did not survive for more than 4 days at this humidity. At 45% relative humidity, and at all relative humidities up to 85%, development is possible, which shows that development cannot take place at as low relative humidities at 100° F. as at 90° F. or 80° F. At 95% relative humidity hoppers failed to reach the adult stage. Optimum development occurs between 60% and 65% relative humidity at 100° F.

Only one experiment has been completed on *Locusta* at 110° F. (43·3° C.) and at what I consider to be the optimum relative humidity (65%). Judging from the time required for hopper development this hypothesis would seem to be fairly correct.

Experiments on *Schistocerca* hoppers at the three temperatures 80° F. (26·7° C.), 90° F. (32·2° C.) and 100° F. (37·8° C.), (Table 2) show that the range

Table 2.

Schistocerca gregaria.

Table showing the effect of humidity and temperature on the rate of hopper development and the percentage of hoppers becoming adult.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of hoppers.	Length of hopper life.						No. of hoppers becoming adult.		% of hoppers becoming adult.
					Average.		Min.		Max.				
					♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	
26	27.v.35	80° F. (26·7° C.)	25	41	—	—	—	—	—	—	All dead by 4th day.		
25	31.iii.35		35	18	41·0	—	41	—	41	—	*1	0	5·5
12	2.ii.35		60	125	42·2	42·6	38	38	49	48	37	45	65·7
5	8.x.34		75	46	35·3	36·3	34	35	36	37	7	6	18·8
24	16.ii.35		85	189	37·8	37·1	32	34	38	39	14	8	11·6
S.C.	11.v.35	90° F. (32·2° C.)	35	38	—	—	—	—	—	—	All dead by 3rd day.		
22	1.x.34		45	24	30·0	27·8	30	27	30	29	1	6	29·2
22	1.viii.34		50	42	27·8	31·7	26	30	32	33	6	7	31·0
24	7.viii.34												
18	24.ii.34		60	46	26·3	27·3	26	26	27	28	6	15	45·7
17	29.v.35		65	20	27·3	27·6	26	26	28	29	3	10	65·0
20	16.xi.33		70	46	27·7	27·7	25	26	31	31	12	16	60·9
25	27.ix.35												
11	8.xii.34		75	59	31·1	33·2	28	32	35	36	8	4	20·4
18	15.x.34												
18	6.ii.35		80	141	—	—	—	—	—	—	All dead by 18th day.		
19	26. i.34		85	89	—	—	—	—	—	—	All dead by 11th day.		
J	9.iv.34												
15	16.ii.35		90	13	—	—	—	—	—	—	All dead by 4th day.		
12	9.xi.34	100° F. (37·8° C.)	35	43	—	—	—	—	—	—	All dead by 3rd day.		
22	1.viii.34		45	41	28·0	—	27	—	30	—	3	0	7·3
1	28.i.34		50	47	27·8	28·7	26	27	30	30	5	6	23·8
27	2.x.34		55	37	24·3	24·3	22	23	27	27	12	9	56·8
29	11.v.35		65	37	25·5	25·8	23	24	27	28	11	11	59·5
8	19.x.34		70	38	22·4	23·6	21	22	24	25	7	5	31·6
20J	28.i.34		80	43	—	—	—	—	—	—	All dead by 23rd day.		
J	23.ii.34		85	—	—	—	—	—	—	—	All dead in a few days.		

* The majority of hoppers died during the first 3 days.

of relative humidities suitable for development is much smaller than for *Locusta* hoppers.

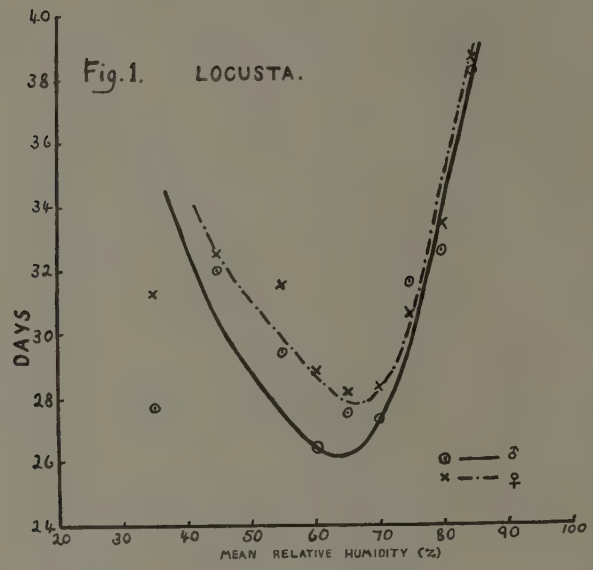
At 80° F. (26·7° C.) and at relative humidities from 25% to 85% the results are very similar to those for *Locusta* at this temperature, *i.e.* hoppers fail to reach the adult stage at 25% relative humidity but succeed at all relative humidities ranging from 35% to 85%.

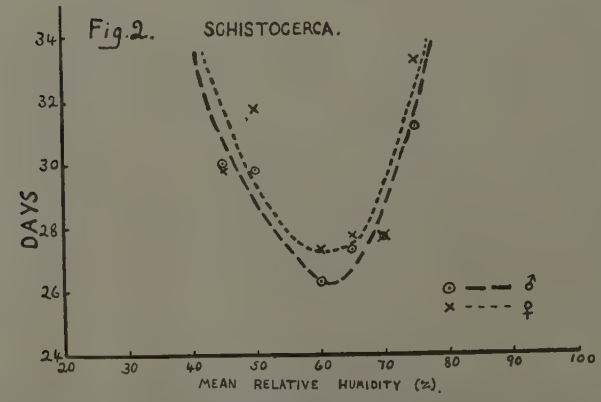
At 90° F. (32·2° C.) hoppers fail to reach the adult stage at 35% relative humidity but succeed at 45% and at all relative humidities between this and 75%. With an increase of the relative humidity to 80% and then to 85% and 90%, the hoppers were not only unable to complete their development but showed a gradual reduction in the time during which they were able to withstand this rise in humidity. This indicates a marked difference in the reaction of the two species to humidity, as *Locusta* hoppers were able to complete their development at relative humidities between 35% and 85% at 90° F.

Experiments at 100° F. (37·8° C.) also show that *Schistocerca* is unable to complete its development over as wide a range of relative humidity as *Locusta*. At 35% all the hoppers died in a few days, but at 45% a small percentage developed into adults. Above this humidity the rate of development increased as the relative humidity increased until 70% was reached, optimum development taking place between 55% and 70%. At 80% relative humidity hoppers are able to survive for a considerable time and partly develop but fail to reach the adult stage. Unfortunately, no experiments were carried out at 75% relative humidity, but judging from the results at 70% and 80% I think it likely that development could take place at 75%. This being so the range of relative humidities for *Schistocerca* at 100° F. would be the same as at 90° F. These results show that *Schistocerca* at 100° F. is able to withstand approximately the same low humidity as *Locusta* but is unable to survive and develop at as high a relative humidity.

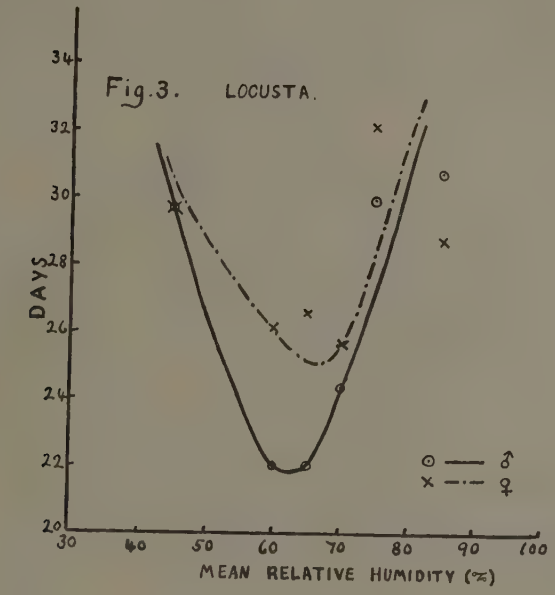
This difference of the two species at 90° F and 100° F. is further demonstrated in curves showing the effect of relative humidity on the rate of development at these temperatures (figs. 1 to 4). It should be noted that the decrease in the rate of development is much greater when the humidity is increased above the optimum than when it is reduced by a corresponding amount below it. It may be assumed from these results that at the higher humidities there is an accumulation of water in the body which inhibits development (*cf.* Buxton and Lewis 1934), whereas at the low humidities it is desiccation (*cf.* Gunn 1933 and 1934) which causes the inhibition. Further, it should be pointed out that the time required to reach the adult state varies from the mean, more as the humidity increases above the optimum conditions than it does when the humidity decreases below the optimum conditions.

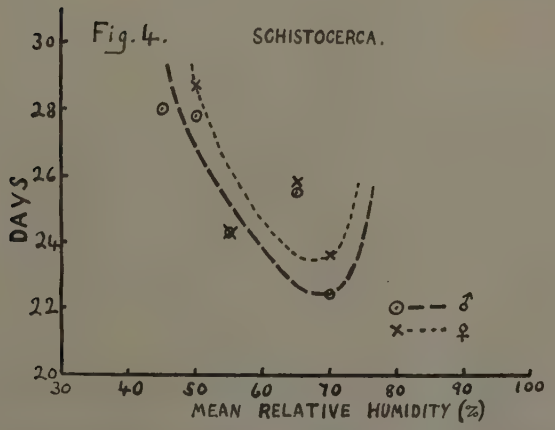
It is very difficult to make definite statements regarding *Nomadacris* (Table 3), since this species has a much longer life-cycle and the number of experiments completed is much smaller. It is possible, however, to say that at 30% relative humidity and 80° F. (26·7° C.) all hoppers died in a few days. The only other experiment at 80° F. was at 75% relative humidity when a very small percentage reached the adult stage. At 90° F. (32·2° C.) neither the upper nor the lower limits of humidity have been reached, but at 100° F. (37·8° C.), 75% relative humidity appears to be the maximum limit. In one experiment a small percentage of hoppers developed into adults while in another experiment none succeeded in reaching the adult stage. At 100° F. it is impossible to rear *Nomadacris* at as low a relative humidity as 40%. I believe that the optimum relative humidity is between 60% and 70%, since under these conditions the





FIGS. 1–2.—The effect of relative humidity at 90° F. on the length of hopper life of male and female: (1) *Locusta migratoria migratorioides*; (2) *Schistocerca gregaria*.





FIGS. 3–4.—The effect of relative humidity at 100° F. on the length of hopper life of male and female: (3) *Locusta migratoria migratorioides*; (4) *Schistocerca gregaria*.

rate of development was faster and the percentage of hoppers becoming adult was higher than at any other humidity.

It must be remembered that some of the experiments on *Nomadacris* hoppers (as indicated in Table 3) were carried out with hoppers which were the progeny of adults whose sexual development had been accelerated (see p. 43) and this in some way may have reduced their vitality.

Table 3.

Nomadacris septemfasciata.

Table showing the effect of humidity and temperature on the rate of hopper development and the percentage of hoppers becoming adult.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of hoppers.	Length of hopper life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.	No. of hoppers becoming adult. ♂.	No. of hoppers becoming adult. ♀.	% of hoppers becoming adult.	Remarks.
25	18.iii.35	80° F. (26·7° C.)	30	50	—	—	—	—	—	—	—	—	0	F_1
26	9.iii.35		75	300	52·0	52·7	45	49	56	57	6	7	4·3	F_1
B.	24.iii.34	90° F. (32·2° C.)	55	—	50·2	49·8	45	47	52	52	15	8	—	F_1
18	26.ix.34		70	25	46·4	50·5	43	43	56	56	10	12	88·0	F_x*
20	12.ix.34		70	—	73·0	66·5	73	60	73	73	1	2	—	F_4
8	30.iv.34		75	100	54·0	53·8	45	39	63	63	5	7	12·0	F_3
15	2.iii.35		75	60	51·0	46·3	40	42	60	62	13	7	33·3	F_1
12	11.vi.34	100° F. (37·8° C.)	40	41	—	—	—	—	—	—	—	—	0	F_3
30	14.viii.34		65	—	52·0	52·5	52	50	52	55	1	2	—	F_4
11	7.iv.35		70	150	40·0	39·0	36	34	44	44	3	4	4·7	F_1
29	26.ix.34		70	37	43·4	38·6	40	37	48	44	9	5	37·9	F_x*
12	31.iii.34		75	—	60·7	71·5	55	71	72	72	8	2	—	F_3
1	18.vii.34		75	72	—	—	—	—	—	—	—	—	0	F_2

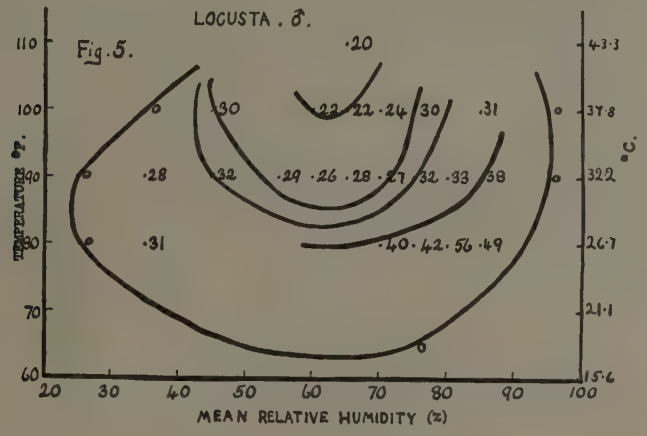
* F_x progeny of ♂ Stock I F_3,x ♀ Stock II F_1.

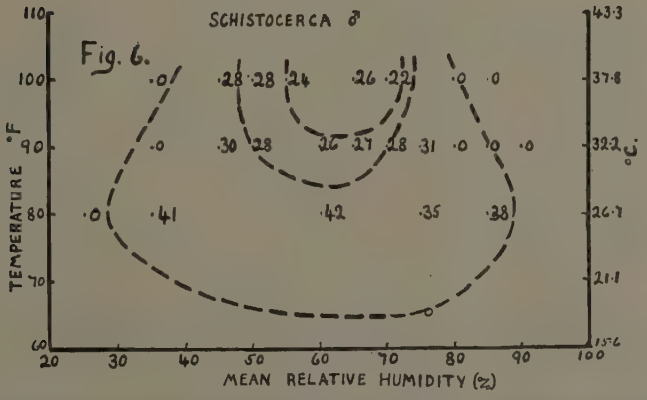
(b) *Temperature.*

The lowest constant temperature at which it has been possible, up to the present date, to rear locusts successfully is 80° F. (26·7° C.). Experiments using *Locusta* and *Schistocerca* hoppers were started at laboratory temperature (60° F. (15·6° C.) to 70° F. (21·1° C.) according to the time of year) and at the optimum humidity conditions, but they died during the first or second instar. As these experiments showed the impossibility of newly emerged hoppers developing at this low temperature, it was decided to try *Locusta* hoppers which had been kept at 90° F. and 60% relative humidity until the 5th instar and then place them in a cage at laboratory temperature, the relative humidity remaining approximately the same as before. It was found in an experiment using 4♂ and 4♀ hoppers that only 1♂ and 1♀ reached the adult stage and they died in 6 and 11 days respectively, without having become sexually mature. The other hoppers, although they failed to moult into the adult stage, lived on the average 11·5 days. The minimum length of life after being transferred to the lower temperature was 3 days and the maximum 23 days.

It may be seen from Tables 1 to 3 that the rate of development, at optimum relative humidity increases with the rise in temperature, but as the relative humidity varies with temperature, curves showing the effect of temperature alone are unsatisfactory, and for this reason graphs showing lines of equal velocity have been made. In order to avoid too many points around the centre of the graphs, curves are given for ♂ and ♀ separately. When constructing these curves it is impossible, owing to individual variation, to join all points of equal

velocity together as it is necessary to be guided by the general trend of the results. As there are several points at some temperatures where the hoppers failed to become adult, the points joined are those where death occurred in less than a week. There is no apparent difference in the two sexes and it is clearly demonstrated that there is a central portion where the rate of develop-

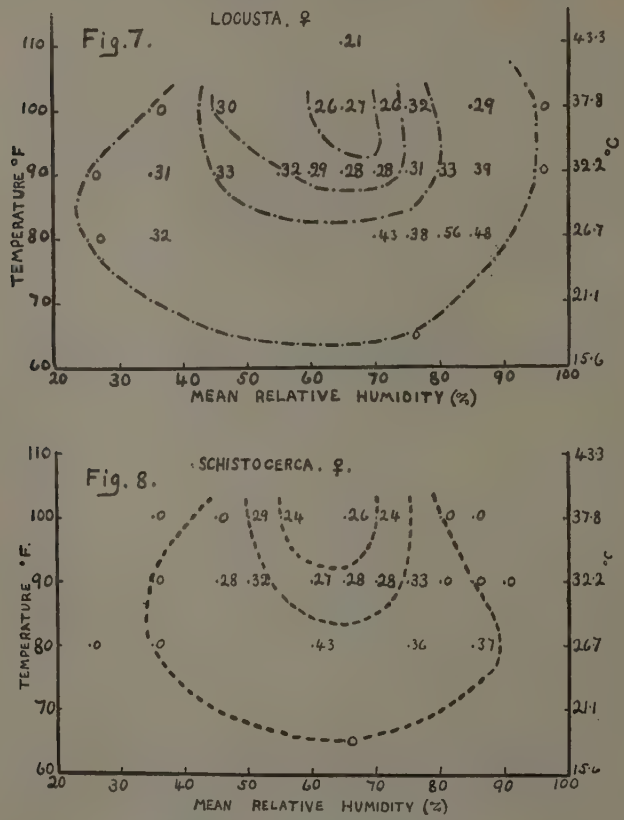




FIGS. 5–6.—Lines showing equal length of hopper life of males at different relative humidities and temperatures: (5) *Locusta migratoria migratorioides*; (6) *Schistocerca gregaria.*

ment is fastest. Comparing the two species, there is sufficient evidence to show that the central portion of optimum development is at a higher temperature for *Locusta* than *Schistocerca.* This is suggested by reason of the fact that the lines on the *Locusta* figures are still widening out as they pass the 100° F. line whereas in the *Schistocerca* figures they are closing. In figs. 5 to 8 it may be seen that the optimum range of relative humidity is greater for *Locusta* than for *Schistocerca.*

The effect of temperature on the development of *Nomadacris* hoppers is still very imperfectly known as may be seen from Table 3. In one experiment at 80° F. development was slower than in some experiments at 90° F. while it was faster in other experiments than at 90° F. A similar comparison may be made with regard to hoppers reared at 100° F. Attention must be drawn to the fact



FIGS. 7–8.—Lines showing equal length of hopper life of females at different relative humidities and temperatures: (7) *Locusta migratoria migratorioides*; (8) *Schistocerca gregaria*.

that in one experiment at 100° F. and 70% relative humidity (Ref. No. 11, 7.iv.35) the fastest development on record was obtained. It should be observed that this experiment was carried out with F_1 individuals, a point to be borne in mind when comparing the other results. With regard to the number of adults which emerged it may be seen that the highest percentage, for any one experiment, was produced at 90° F., but, all things considered, 100° F. appears to be the most suitable.

IV. The Effect of Constant Humidity and Constant Temperature on the Percentage of *Locusta* and *Schistocerca* Hoppers Becoming Adult.

Humidity plays an important part in controlling the percentage of hoppers that become adult (Tables 1 and 2). Figs. 9–11 show curves of the two species at three different temperatures; owing to the lack of sufficient data it is possible to represent only approximately the peak of the curves at 80° F. It should be noted that at 90° F. and 100° F. the peaks are at a different relative humidity.

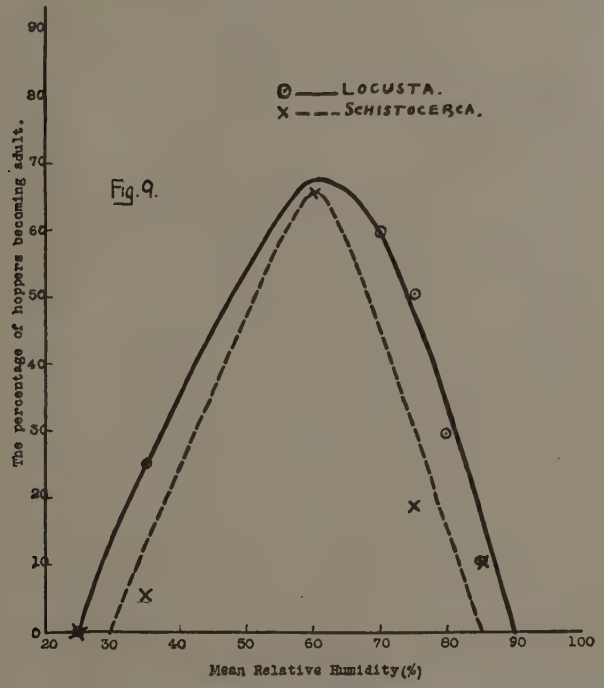


Fig. 9.—The effect of relative humidity on the percentage of hoppers of *Locusta migratoria migratorioides* and *Schistocerca gregaria* becoming adult at 80° F.

In fig. 10, at 90° F. the peaks are between 65% and 70% relative humidity while in fig. 11, at 100° F., they are between 60% and 65%. Furthermore, the peak varies with the species, being at a slightly higher humidity for *Locusta* than *Schistocerca*. Perhaps the most striking feature of these figures is the manner in which the curves for *Schistocerca*, at all three temperatures, fit inside the curves for *Locusta*, thus emphasising the narrower range of conditions at which *Schistocerca* is capable of developing. Another point worthy of attention is shown in Table 2. Here it may be seen that at a relative humidity of 80% all the *Schistocerca* hoppers died without becoming adult, but some lived as long as 18 days. Then, as the humidity is increased to 85% and 90%, the maximum life of the hoppers is reduced to 11 and 4 days respectively.

In order to compare the effect of temperature on the percentage of hoppers becoming adult it is necessary to construct lines of equal percentage (figs. 12, 13). In this case it has been possible to continue several of the curves until they meet, thus forming a circle around the optimum zone. It may be seen that the optimum temperature for *Locusta* appears to be slightly above 90° F. and for *Schistocerca* slightly below. Unfortunately, in the case of *Schistocerca* the figure which falls in the centre of the lines of equal percentage is 46%, which is too low. As this is surrounded by higher percentages and as it does not fit properly in the other curve (fig. 10) it may be regarded as an abnormal variation.

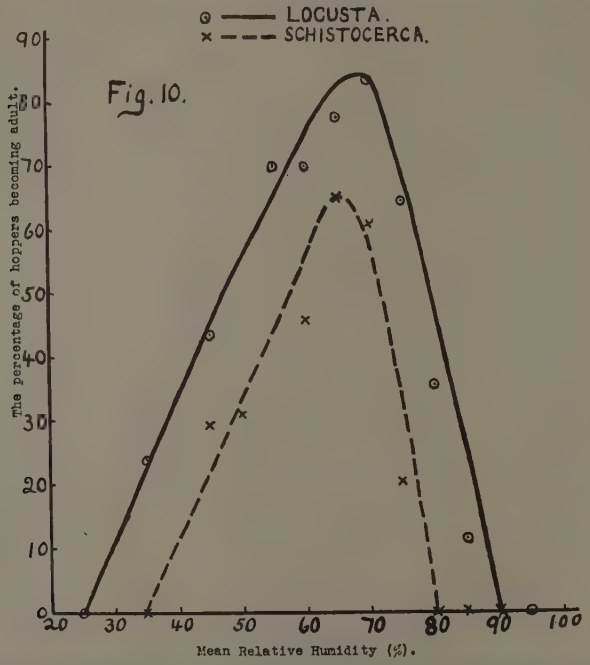


Fig. 10.—The effect of relative humidity on the percentage of hoppers of *Locusta migratoria migratorioides* and *Schistocerca gregaria* becoming adult at 90° F.

V. The Effect of Constant Temperature and Variable Humidity on Hopper Development.

Experiments carried out under these conditions show that it is the early hopper stages which are most affected by the extreme conditions of relative humidity. If experiments 5 and 6 on *Locusta* (Table 4) be considered, it may be seen that individuals kept at 100° F. under optimum humidity conditions for the first 20 days of their development, gave a much higher percentage of adults (25·5 and 31·5) when the humidity was reduced to 45% during the remainder of the developmental period than did individuals which had been kept at 45% relative humidity from the time of hatching (Table 1, Ref. No. 12, 10.xii.34).

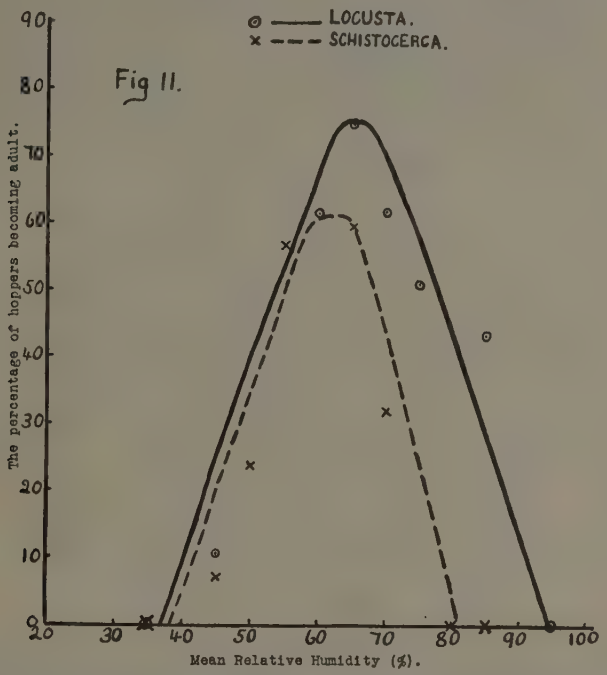


FIG. 11.—The effect of relative humidity on the percentage of hoppers of *Locusta migratoria migratorioides* and *Schistocerca gregaria* becoming adult at 100° F.

TABLE 4.

Locusta migratoria migratorioides.

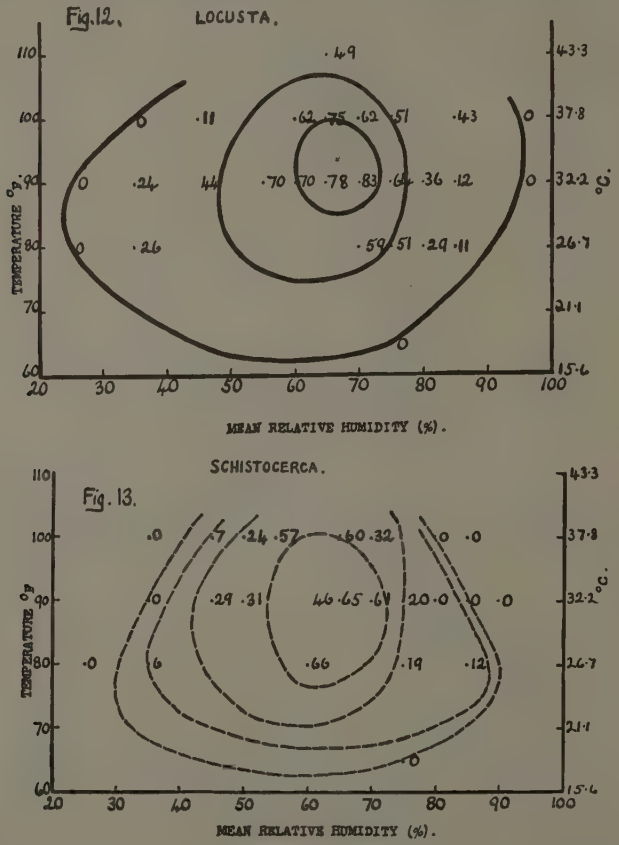
Length of hopper life at constant temperatures and humidities, the humidity being altered after a period.

Ref. No.	Date.	Temp. °F.	Mean R.H., %.	No. of hoppers.	Length of hopper life.						No. of hoppers becoming adult.		% of hoppers becoming adult.
					Average.		Min.		Max.				
					♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	
5	11.ii.34	100	70 for 20 days then 45	156	34·1	32·6	25	29	40	40	23	17	25·5
6	15.iii.34	100	70 for 20 days then 45	92	34·4	38·1	25	25	49	51	17	12	31·5

A point to be noted in this connection is the time required to reach the adult stage. The first individuals to become adult were very little affected compared with the later individuals, when the time required was much longer than the average. The variation was much greater than is usually found, from which I conclude that the reduced humidity had little effect on the individuals about to moult while in the others it appears to have checked the rate of development very considerably. (Note: The percentage of hoppers reaching the adult stage is

calculated from the total at the commencement of the experiment and not from the number present when the humidity was reduced.)

The experiments on *Schistocerca* (Table 5) were conducted over a wider range of conditions. The second experiment (Ref. No. 12, 7.vii.34) was at 100° F., the humidity being 70% for the first 7 days, then being reduced to 35%. It was



FIGS. 12–13.—Lines showing equal percentage of hoppers becoming adult at different relative humidities and temperatures: (12) *Locusta migratoria migratorioides*; (13) *Schistocerca gregaria*.

found that 5% developed into adults, whereas if newly emerged hoppers were placed in a humidity of 35% at this temperature, they always died in a few days (*cf.* Table 2). The percentage of adults, as in the case of *Locusta*, was calculated from the number of hoppers when the experiment was started at the optimum humidity. Perhaps the most interesting experiments are Nos. 13, 5 and 8 at 25%, 50% and 80% respectively (Table 5), where the hoppers were all kept at

100° F. and 55% for the first 7 days. They were then divided into lots of 100 each and placed in cages at the above-mentioned humidities. The percentage of adults in these cages is calculated from the number when the humidities were changed and does not take into account those which died under optimum conditions. This shows that at 25% relative humidity, which is much lower than newly emerged hoppers could withstand, 7·0% completed development at only

TABLE 5.

Schistocerca gregaria.

Length of hopper life at constant temperatures and humidities, the humidity being altered after a period.

Ref. No.	Date.	Temp. ° F.	Mean R.H., %.	No. of hoppers.	Length of hopper life.						No. of hoppers becoming adult.		% of hoppers becoming adult.
					Average.		Min.		Max.				
					♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	
3	34.x.34	80	60 for 7 days then 85	36	34·8	40·5	33	35	37	44	6	4	27·7
12	7.vii.34	100	70 for 7 days then 35	80	29·3	27·0	27	27	31	27	3	1	5·0
13	2.iv.34	100	55 for 7 days then 25	100	27·7	28·0	27	28	28	28	6	1	7·0
5	2.iv.34	100	55 for 7 days then 50	100	26·7	27·3	23	25	31	31	16	9	25·0
8	2.iv.34	100	55 for 7 days then 80	100	28·0	—	28	—	28	—	2	0	2·0

a slightly reduced rate. Those reduced to 50% relative humidity gave a slightly higher percentage of adults (25·0) than did individuals kept at 50% relative humidity (*cf.* Table 2) throughout the entire development period. The length of hopper life was about normal. In the case of those where the relative humidity was increased to 80%, the number of hoppers becoming adult was 2% as compared with 0% when newly emerged hoppers were subjected to this humidity.

In one experiment carried out at 80° F. the relative humidity was increased from 60% to 85% on the 7th day. This had no effect on the length of hopper life (*cf.* Table 2), but 27·7% became adult as compared with 65·7% at a relative humidity of 60% and 11·6% at a relative humidity of 85%.

VI. The Effect on Hopper Development of Humidity and Temperature Fluctuating Day and Night.

Because a reduction in temperature, in enclosed cages, means a rise in the relative humidity it is impossible to carry out experiments of this nature without considering both factors together. In these experiments the temperature was maintained at 100° F. between 10 a.m. and 5 p.m. and 80° F. for the remainder of the 24 hours. Speaking generally, for air with a constant moisture content, this means a variation of approximately 30% in the relative humidity.

At the above-mentioned temperatures and at humidities ranging from 60% to 90%, according to change in temperature (Table 6), the time required for *Locusta* hopper development was approximately the same as in experiments at 90° F. and 75% relative humidity. However, it should be remarked that a larger percentage became adult. In another experiment where the relative humidity alternated from 55–85%, the length of hopper life was also approxi-

mately the same as at the mean of the conditions, but the percentage which became adult was much lower.

TABLE 6.

Locusta migratoria migratorioides.

Table showing the length of hopper life at different humidities and temperature; day and night.

Ref. No.	Date.	Temp. D. N.	Mean R.H., %. D. N.	No. of hoppers.	Length of hopper life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.	No. of hoppers becoming adult. ♂.	No. of hoppers becoming adult. ♀.	% of hoppers becoming adult.
4	29.iv.35	100–80	55–85	84	30·0	31·9	25	27	35	35	16	16	38·1
4	29.i.35	100–80	60–90	27	28·2	30·0	27	29	32	32	11	9	83·3

For *Schistocerca* (Table 7) there is an upper limit of humidity, corresponding to that of the different temperatures where development is arrested, and, at these humidities, death takes place after a certain period. It was found that

TABLE 7.

Schistocerca gregaria.

Table showing the length of hopper life at different humidities and temperature; day and night.

Ref. No.	Date.	Temp. D. N.	Mean R.H., %. D. N.	No. of hoppers.	Length of hopper life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.	No. of hoppers becoming adult. ♂.	No. of hoppers becoming adult. ♀.	% of hoppers becoming adult.
4	7.iii.35	100–80	60– 90	33	31·0	29·8	28	29	34	30	12	5	51·5
5 4	26.i.35 } 9.vi.35 }	100–80	65– 95	98	33·6	34·5	29	29	38	39	20	13	33·6
29	17.vi.35	100–80	70–100	47	45·0	46·5	37	37	55	53	7	4	23·4
3	21.i.35	100–80	75–100	30	—	—	—	—	—	—	All dead by 21st day.		

as the humidity was reduced the results were very similar to those at 90° F. and at a relative humidity approximately the mean of the variation.

One experiment was carried out with *Nomadacris* under these conditions, but as the number of experiments under constant conditions is very small it is impossible to draw any conclusions.

VII. Sexual Maturation of Adults.

(i) *Locusta* and *Schistocerca*.

(a) *Sexual development of adults under approximately the same constant humidity and temperature as those at which the hoppers were reared.*

In experiments with adults it is not sufficient to compare the effect of humidity and temperature on the adults alone, but it is necessary to consider the humidity and temperature at which the hoppers were reared. Throughout this paper the term sexual maturity refers to the production of the first egg-pod, and the time required to reach sexual maturity is calculated from the emergence

of the adult until that time. This, however, means that sexual maturity in the males has occurred a few days earlier but, as it is not always possible to be definite as to when pairing first took place, the first egg-pod is taken as the standard. Where possible pairing is recorded. The mean optimum relative humidity which produces the earliest sexual maturation varies with the species and temperature, as may be seen from Tables 8–11.

Experiments at laboratory temperature (65–70° F.) were carried out at relative humidities 45–80% (Tables 8 and 10). As neither species attained sexual maturity at any humidity, I consider the temperature to be the inhibiting factor. It should be noted that these adults emerged at 90° F. and at the optimum relative humidity.

Table 8.

Locusta migratoria migratorioides.

Table showing the effect of humidity on sexual maturation, fecundity and length of adult life at laboratory temperature (65–70° F.).*

Ref. No.	Date.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	♀.	Min. ♂.	♀.	Max. ♂.	♀.
22	4.xi.34	45	4	4	—	—	0	0	14·8	10·2	11	7	18	13
21	6.xi.34	80	7	2	—	—	0	0	9·0	5·5	1	6	12	7
22	24.ii.34	80	7	10	—	—	0	0	† 60·1	71·0	19	19	102	113

* Emerged at 90° F. and optimum relative humidity.
† These individuals were kept at 90° F. and 55% relative humidity for 9–10 days after emergence. The ages given do not include this time.

Table 9.

Locusta migratoria migratorioides.

Table showing the effect of humidity and temperature on sexual maturation, fecundity and length of adult life.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* days.	1st egg-pod laid, days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	♀.	Min. ♂.	♀.	Max. ♂.	♀.	Remarks.
25	4.iv.35	80° F. (26·7° C.)	35	13	18	—	—	0	0	28·2	23·6	1	8	64	53	F_2
22	6.iv.35		70	15	7	—	27	11	1·6	28·6	46·0	9	9	64	80	F_2
9	20.vi.34		75	5	4	25	35	8	2·0	50·0	62·8	4	12	111	111	F_2
9	12.xii.33		80	4	10	—	31	37	3·7	128·8	113·0	60	68	179	139	F_1
19	3.iv.35	90° F. (32·2° C.)	35	5	6	—	—	0	0	29·8	40·5	20	18	58	57	—
15	22.iv.35		60	11	8	24	25	7	1·8	49·3	47·6	26	25	67	65	—
13	27.vi.34		60	12	8	—		22		44·5	54·8	5	5	78	97	—
27	14.viii.34		65	6	7	15	20	15	2·1	34·5	30·6	13	20	61	57	—
26	2.x.34		70	4	3	20	21	21	7·0	23·0	51·6	6	31	*35	68	—
19	30.i.35		75	3	1	20	24	6	6·0	73·0	68·0	65	68	82	68	—
16	17.iii.35		85	7	9	19	40	15	1·7	71·9	74·3	26	59	121	86	—
13	12.x.33	100° F. (37·8° C.)	40	6	6	15	43	2	0·33	35·2	43·5	6	5	54	65	—
12	9.i.35		45	2	2	16	22	2	1·00	25·5	23·0	23	22	28	24	—
11	29.vi.33		55	19	12	14	21	14	1·20	36·4	47·4	2	2	78	77	—
4	5.ix.34		60	7	5	13	15	15	3·00	72·4	45·0	28	19	95	62	—
11	20.viii.35		70	4	6	10	12	19	3·17	25·3	32·2	15	17	*46	51	—
12	1.xi.34		75	5	4	9	14	9	3·20	22·4	30·5	4	15	33	42	—
6	29.viii.34		75	10	5	10		20		39·5	43·6	20	32	71	81	—
12	12.ix.33		80	8	5	13	24	3	0·60	31·4	26·8	20	6	41	41	—

* When the last ♂ in the experiment died other mature ♂♂ were added.

Owing to the time required to complete experiments at 80° F. and the fact that it is only possible to maintain this low temperature during the winter months, the number of experiments was limited. In the case of *Locusta*, the variation at high relative humidities is too wide to permit of any conclusions being drawn, but at low humidity (35%) sexual development is inhibited. On the other hand, *Schistocerca* appears to be more constant in the length of time required to reach sexual maturation at high humidities. Humidities over 80% are detrimental.

Table 10.

Schistocerca gregaria.

Table showing the effect of humidity on sexual maturation, fecundity and length of adult life at laboratory temperature (65–70° F.).*

Ref. No.	Date.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	♀.	Min. ♂.	♀.	Max. ♂.	♀.
31	2.v.34	45	5	5	—	—	0	0	78·8	49·2	19	4	147	150
32	2.v.34	80	5	5	—	—	0	0	27·2	42·4	3	21	68	99

* Emerged at 90° F. and optimum relative humidity.

As the relative humidity is reduced the rate of sexual development is gradually retarded until a low limit is reached where it is prevented. Here, as at the upper limit, there is a slight difference in the response of the two species. At 35% relative humidity it is possible to rear a considerable number of *Locusta* to the adult stage, although sexual maturation never occurred, but with *Schistocerca* the percentage of adults was so small that it was impossible to continue the experiment during the adult stage.

Table 11.

Schistocerca gregaria.

Table showing the effect of humidity and temperature on sexual maturation, fecundity and length of adult life.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	♀	Min. ♂.	♀.	Max. ♂.	♀.
21	12.xi.34	80° F. (26·7° C.)	75	7	6	—	59	12	2·00	122·7	123·5	49	81	189	198
23	29.xi.34		80	3	4	—	58	3	0·36	36·6	53·5	1	4	73	76
10	13.iii.35		80	8	10	—	46	2		51·4	50·0	28	25	65	63
24	23.iii.35		85	8	7	—	—	0	0	10·5	48·7	1	2	76	92
17	6.v.34	90° F. (32·2° C.)	40	15	11	83	132	6	0·55	108·7	146·4	1	1	261	254
16	8.x.34		65	3	7	—	38	32	4·58	156·3	132·0	132	80	187	189
18	17.iii.34		70	5	12	15		17		32·1	41·8	9	4	55	129
11	8.i.35		70	3	2	22	24	2	1·82	33·4	30·0	13	27	54	33
20	12.xii.33		70	1	3	—		11		110·0	58·6	110	37	110	70
16	6.x.33		75	4	3	26	30	2	0·66	38·0	34·0	3	10	80	54
18	21.ix.33		80	2	6	—	35	2	0·33	60·0	59·0	1	4	139	138
6	27.iv.34	100° F. (37·8° C.)	45	4	3	47	55	7	2·33	74·0	69·3	57	65	97	72
1	26.viii.34		55	5	5	21	22	15	3·00	46·6	45·4	42	29	53	64
8	12.xi.34		65	6	5	—	19	12	2·50	42·5	57·2	23	30	72	112
11	25.x.34		70	8	7	13	19	7	1·00	25·8	19·3	4	4	39	64
5	26.ix.33		75	9	4	25	33	4	1·00	26·1	17·8	4	2	69	45
10	3.v.34		80	9	4	50	55	7	1·75	36·0	42·5	2	2	130	95

Regarding the effect of different constant humidities at 90° F. it may be seen that there is a larger range of optimum relative humidity for *Locusta* than for *Schistocerca*. This is clearly shown in fig. 14.

When experiments were carried out on adults at 100° F. and at approximately the same humidity as those at which the hoppers had been reared, the range of humidities (fig. 15) is small since it is impossible to rear hoppers at as low, or as high, a humidity, at this temperature, as at 80° F. and 90° F. For reasons which will be discussed later (see p. 40), it is possible only to include experiments on the

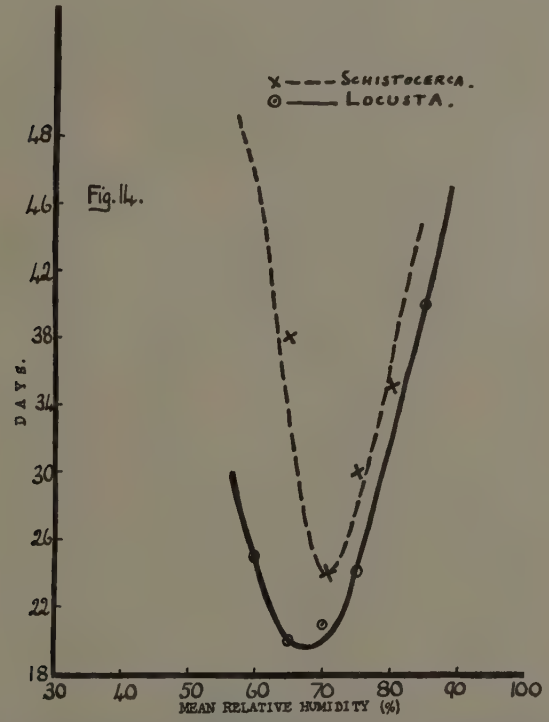


FIG. 14.—The effect of relative humidity on the rate of sexual development of *Locusta migratoria migratorioides* and *Schistocerca gregaria* at 90° F. (Expressed as the number of days before the first egg-pod was laid.)

(Another point at 40% and 132 days on the *Schistocerca* curve is not indicated.)

F_1 generation of *Schistocerca* at 100° F. It may be seen (Tables 9 and 11) that the range of humidity for *Locusta* is from 45% to 80% and within these limits the variation in the time required for sexual maturation is slight. *Schistocerca* shows a smaller range, 55% to 75% but a more marked variation.

When comparing the curves of the rate of sexual maturation and humidity at 90° F. and 100° F. (figs. 14 and 15) it should be noted, as in the case of the hoppers (see p. 15), that the curve for *Schistocerca* fits inside that for *Locusta*. Another point worthy of attention is the sudden increase in the time required to

reach sexual maturation when the humidity is increased above the optimum compared with the more gradual curve produced when the humidity is reduced.

The effect of temperature on the two species is shown in figs. 16 and 17. It has been possible only to construct a few lines for *Locusta*, and even these do not fit perfectly as there is a much greater variation than in the case of *Schisto-*

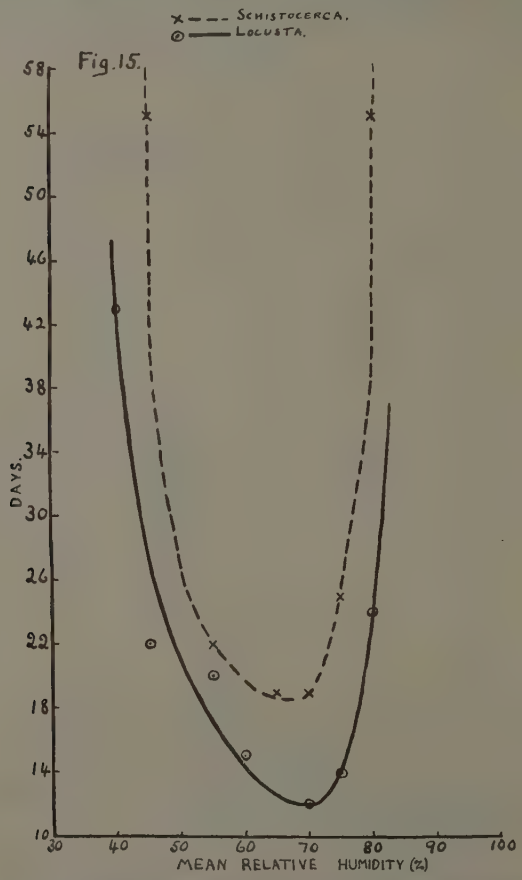


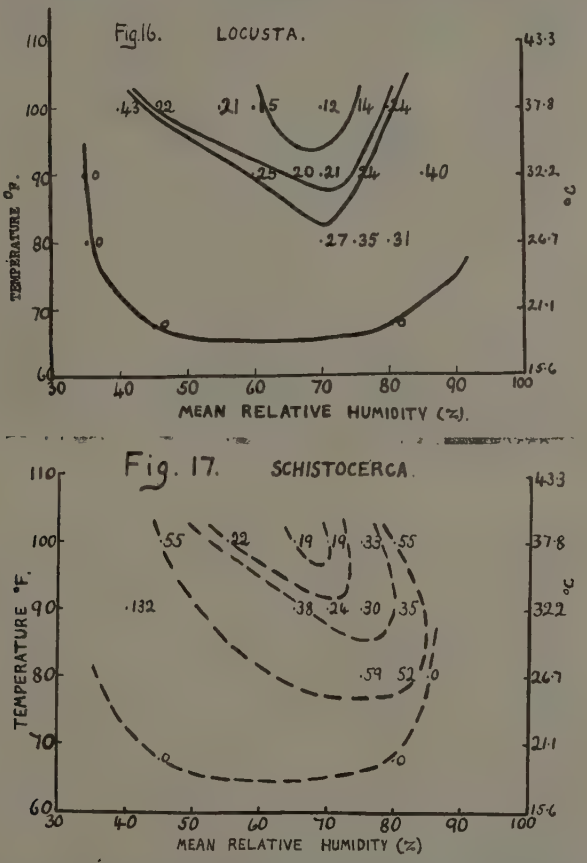
FIG. 15.—The effect of relative humidity on the rate of sexual development of *Locusta migratoria migratorioides* and *Schistocerca gregaria* at 100° F. (Expressed as the number of days before the first egg-pod was laid.)

cerca. In *Locusta* the lines appear to rise fairly evenly, both ends pointing outwards up to 100° F. while in *Schistocerca* there is a definite movement towards a lower optimum humidity at the higher temperatures. From these figures it would appear that 100° F. is the optimum for both species, but it will be seen later (see p. 40) that *Schistocerca* is unable to breed continuously at so high a temperature.

(b) *Hoppers reared under optimum humidity, adults kept at low humidity.*

In order to compare still further the effect of low humidity on the two species, hoppers were reared at optimum humidity conditions and as the adults emerged they were transferred to a low humidity.

At 80° F. (Table 12) one experiment was carried out with *Locusta*, and one



FIGS. 16–17.—Lines showing equal velocity of the rate of sexual development at different relative humidities and temperatures. (Expressed as the number of days before the first egg-pod was laid.) (16) *Locusta migratoria migratorioides*; (17) *Schistocerca gregaria*.

with *Schistocerca*. In both cases the hoppers were reared at 80° F. and at optimum relative humidity. The adults in the *Locusta* experiment were kept at 30% relative humidity; it was found that pairing took place after 60 days and oviposition after 66. This is more than twice the time required under optimum humidity, but shows that they were capable of reproducing, though the fecundity was greatly reduced at this low humidity. In the experiment on *Schistocerca* at 35% relative humidity pairing and oviposition did not take

place although the length of adult life was much longer than under optimum conditions. This shows that *Locusta* is capable of becoming sexually mature at a lower relative humidity than *Schistocerca*.

TABLE 12.

Table showing the effect of rearing *Locusta* and *Schistocerca* at 80° F. (26·7° C.) and optimum humidity; the adults on emergence being transferred to a lower humidity as shown below.

Ref. No.	Date.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average ♂.	Average ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.
Locusta migratoria migratorioides.														
25	10.xi.34	30	4	10	60	66	2	0·2	36·5	58·2	13	6	80	98
Schistocerca gregaria.														
13	15.iii.35	35	14	13	—	—	0	0	129·6	177·3	42	8	247	258

In the case of *Locusta* at 90° F. it was found necessary to reduce the humidity to 25% (Table 13) before oviposition was arrested. At this humidity pairing was observed (after 41 days) in one experiment but not in the other. In the experiment in which *Schistocerca* was used it was only necessary to reduce the humidity to 30% in order to arrest both pairing and oviposition. Here again

TABLE 13.

Table showing the effect of rearing *Locusta* and *Schistocerca* at 90° F. (32·2° C.) and optimum humidity; the adults on emergence being transferred to a lower humidity as shown below.

Ref. No.	Date.	Mean R.H., %.	No. of adults. ♂.	♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.
Locusta migratoria migratorioides.														
13	28.ix.35	20	4	6	—	—	0	0	7·8	7·3	3	3	13	17
14	6.ix.34	25	5	7	41	—	0	0	19·2	13·6	8	5	52	57
13	8.x.34	25	2	5	—	—	0	0	5·0	8·2	5	5	5	15
Schistocerca gregaria.														
14	18.iii.34	30	1	2	—	—	0	0	144·0	205·0	144	197	144	213

it may be seen that there is a difference in the two species. *Locusta*, although never having reproduced, died on the average sooner than what is normal under optimum conditions while *Schistocerca* lived much longer than the average under optimum conditions. Further, *Schistocerca* under these dry conditions appears to retain the ability to become sexually mature when suitable conditions arrive. To test this, two pairs of *Schistocerca* were removed from dry conditions (90° F. and 30% relative humidity) at different ages and placed in a suitable atmosphere.

(*a*) The first pair were kept at the low humidity for 98 days and then placed at 75% relative humidity. Copulation occurred after 15 days and an egg-pod

was laid after 24 days (*i.e.* 113 and 122 days respectively from the time of becoming adult). Only one egg-pod was laid and this was on the floor of the cage. The female died after 25 days and the male after 42 days at the high humidity (total 123 and 140 days).

(*b*) The second pair were removed from the low humidity at the age of 123 days and placed at 90° F. and 75% relative humidity. Copulation occurred after 5 days and an egg-pod was laid after 9 days (*i.e.* 128 days and 131 days from the time of becoming adult). Both male and female died after living in the high humidity for 18 days (total 141 days). Only one egg-pod was laid and this, as in the previous case, was deposited on the floor of the cage. Whether the depositing of the egg-pod on the floor was due to too high a humidity or to the decrease in vitality of the female is not known, since in later experiments 75% relative humidity proved to be unfavourable.

Another experiment started on 27.ix.33 with 4 males and 3 females, which had been kept as hoppers under optimum conditions, has proved to be of some

TABLE 14.

Table showing the effect of rearing *Locusta* and *Schistocerca* at 100° F. (37·8° C.) and optimum humidity; the adults on emergence being transferred to a lower humidity as shown.

Ref. No.	Date.	Mean R.H., %.	No. of adults.		1st pair *in cop.*	1st egg-pod laid.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life.					
									Average.		Min.		Max.	
			♂.	♀.	Days.	Days.			♂.	♀.	♂.	♀.	♂.	♀.
Locusta migratoria migratorioides.														
11	10.iv.34	30	7	5	38	41	1	0·20	42·4	15·7	2	6	57	48
11	7.i.34	30	12	7	69	—	0	0	72·3	59·1	2	39	95	94
Schistocerca gregaria.														
11	27.iv.34	35	5	5	—	—	0	0	33·8	39·4	7	1	110	131
5	30.iv.34	35	5	4	—	—	0	0	22·1	21·8	2	3	38	39

interest. The temperature throughout the experiment was 90° F. but the humidity was varied. For the first 21 days the humidity was approximately 70%, then it was gradually reduced to about 35%. By this time 3 males and 1 female had died leaving 1 male and 2 females. Two egg-pods were laid, on the 34th and 42nd day, but whether one was laid by one female and the other by the other female or both by the same female is not known. By the end of 65 days the last male had died. This was 23 days after egg-laying had ceased. Of the two females present when the humidity was reduced, one died at 180 days old and the other at 209 days. When the last male died another male was introduced, but unfortunately, it had been kept at a humidity of 35% all the time, so pairing never occurred. This experiment tends to show that females may become sexually mature under suitable conditions and then, if unfavourable conditions arise before the normal egg-laying period is completed, oviposition is checked and the females live much longer than when the conditions are favourable and oviposition continues uninterruptedly. That the females retain the power to reproduce again is shown by the following experiment:—This experiment started on 6.xii.33 at 100° F. and locusts were kept at a relative humidity of approximately 50% for the first 30 days at which time the humidity was reduced to 30%. On this (30th) day an egg-pod was laid before the humidity was reduced. After 50 days at the low humidity one female

was transferred to a humidity of 75% and mated with a mature male. Copulation took place in 3 days and an egg-pod was laid in 8 days after being transferred to the high humidity. Three more egg-pods were laid by this female before dying at the age of 111 days (31 days after being transferred back to the high humidity). Of the 4 egg-pods laid three gave rise to the average number of hoppers, which shows that fecundity had not been impaired by this enforced diapause. The other female remained at the low humidity for 94 days (total age 124 days) when it was killed. It was found that the ovaries were immature, the first egg in each tube still being small and white.

A comparison with results at 100° F. (Table 14) shows that in the case of *Locusta* a relative humidity of 30% is on the border line, as in one experiment sexual development did not occur, while in the other pairing occurred on the 38th day and oviposition on the 41st day. On the other hand, *Schistocerca* failed to reach sexual maturity in two experiments at a relative humidity of 35%.

(c) *Hoppers reared at an unfavourable humidity, adults kept at optimum humidity.*

A number of *Schistocerca* hoppers were reared at 90° F. and 45% relative humidity; as the adults emerged they were divided into two lots, one at 90° F. and 40% relative humidity and the other at 90° F. and 70% relative humidity. In the case of those at 40% relative humidity oviposition occurred in 132 days, while with those at 70% relative humidity (Table 15) oviposition occurred in 50 days.

TABLE 15.

Table showing the effect of rearing *Locusta* and *Schistocerca* at unfavourable humidity (45%); the adults on emergence being transferred to optimum humidity as shown.

Ref. No.	Date.	Mean R.H., %.	No. of adults. ♂.	No. of adults. ♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.
Schistocerca gregaria at 90° F. (32·2° C.).														
19	31.iv.34	70	10	17	—	50	34	2·00	43·6	70·2	4	4	105	112
Locusta migratoria migratorioides at 100° F. (37·8° C.).														
6	29.ix.33	75	11	6	17	21	15	2·50	75·7	61·2	11	5	98	102
12	15.xi.33	75	2	3	22	30	9	3·00	54·0	49·3	54	30	54	62

This result, in itself, shows that the rate of sexual development was considerably speeded up with the high humidity, but it must also be compared with experiments where both hoppers and adults (Table 11) were kept at 70% relative humidity. Under these conditions oviposition occurred on the average in 24 days after the adults emerged. The important point to be noted here is that the length of hopper life was very little longer at the low humidity than at the optimum humidity, yet sexual maturation must have been greatly retarded when it required 50 days to produce the first egg-pod. In fact this is almost equivalent to the time required to reach sexual maturation plus the time required for hopper development under optimum humidity.

Two experiments on *Locusta* adults which emerged at 100° F. under unfavourable humidity (45%) show a considerable variation in the time required

to reach sexual maturity after being placed under optimum conditions. Both were kept at 100° F. and 70% relative humidity; in one experiment oviposition occurred in 21 days while in the other it required 30 days.

(ii) *Nomadacris.*

(a) *Sexual development of adults under constant and varying conditions of humidity and temperature.*

As the majority of the experiments on the adults of this species were carried out at different humidities and temperatures from those at which the hoppers were reared, the effect of constant and varying conditions are discussed together. Also in many experiments development was considerably speeded up. In order to avoid any unjustified conclusions being drawn, the generation and conditions of humidity and temperature at which the hoppers were kept is given.

At 80° F. only two experiments were completed. These were carried out at 70% and 80% relative humidity (Table 16). If compared with the results obtained on *Locusta* and *Schistocerca* at 80° F. these should be suitable humidities. The insects used in the first experiment (70%) had been kept at the same humidity and at 80° F. during the hopper stages, while in the second experiment (80%) the hoppers were kept at optimum relative humidity and at 100° F. during the day, and 80° F. during the night. In the latter experiment, it is obvious that failure to oviposit was due to the low temperature as the other individuals from the same cage kept at a higher temperature (100° F.) developed sexually and oviposited.

The experiments at 90° F. were conducted over a considerable range of humidities, but oviposition occurred only in one experiment at 70% relative humidity (Table 16). This would suggest that humidity was the principal factor, but two additional experiments were carried out at the same humidity (70%) and in neither cases did oviposition occur. Failure to oviposit in so many experiments over such a range of humidities may be due to (*a*) the fact that 90° F. is an unsuitable temperature and if the humidity is not optimum then sexual development is retarded to such an extent that death occurs before oviposition, or (*b*) the fact that the speeding up of sexual development in the previous generations had reduced the vitality and lowered the power to reproduce. The former hypothesis I consider the most likely as some of the experiments where oviposition never occurred contained the same generation reared during the hopper stage under the same conditions as in experiment No. 11, 16.ix.33 (Table 16) where oviposition did occur. Also in the experiment at 90° F. where sexual development was reached oviposition did not take place until the 81st day, which is more than twice the time required under optimum humidity conditions at 100° F. Another important point to be noted about this experiment is, that during hopper development the temperature was 100° F., the adults on emergence being transferred to 90° F. In all the other experiments on adults at 90° F. where the humidity was suitable, the hoppers had been reared at 90° F. This means that the sexual development (as will be seen later) is much farther advanced when the adults emerge at 100° F. than at 90° F.

It is clearly shown that humidity does affect sexual development by experiment No. 7, 19.v.34 (Table 16) on the first generation bred in captivity under constant conditions. The relative humidity was approximately 85% which is apparently too high as the length of adult life was much shorter than

Table 16.

Nomadacris septemfasciata.

Table showing the effect of relative humidity and temperature on sexual maturation, fecundity and length of adult life.

Ref. No.	Date.	Temp.	Mean R.H., %.	No. of adults. ♂.	No. of adults. ♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average. ♂.	Average. ♀.	Min. ♂.	Min. ♀.	Max. ♂.	Max. ♀.	Temp. at which hoppers were reared. ° F.	Remarks.
23	23.iv.35	80° F. (26·7° C.)	70	3	6	—	—	0	0	20·3	29·3	3	7	52	50	80	S. III. F_1
10	29.ix.33		80	7	8	—	—	0	0	54·0	54·8	3	1	72	94	100–80	S. I. F_2
15	6.x.33	90° F. (32·2° C.)	40	3	9	—	—	0	0	188	203·8	187	188	189	260§	100–80	S. I. F_2
20	24.x.34		65	1	1	—	—	0	0	87	111	87	111	87	111‡	90	S. I. F_4
18	1.vi.34		70	4	2	41	81	3	1·5	64·3	61·0	14	11	126	111	100	S. I. F_3*
18	19.xi.34		70	4	6	—	—	0	0	43·0	50·3	9	7	92	89‡	90	F_x†
17	15.iv.35		70	12	6	—	—	0	0	15·6	16·7	7	7	44	37‡	90	S. III. F_1
7	26.ix.33		80	5	14	—	—	0	0	65·6	85·1	2	3	122	205‡	100–80	S. I. F_2
7	19.v.34		85	3	3	—	—	0	0	16·3	27·0	6	19	29	40‡	90	S. II. F_1
13	9.xi.34	100° F. (37·8° C.)	25	4	1	—	—	0	0	10·2	5·0	4	5	18	5‡	100	F_x†
11	16.ix.33		40‖	2	4	30	38	1	0·25	114·0	99·5	81	62	147	142	100–80	S. I. F_2
30	3.x.34		65	1	2	—	—	0	0	145·0	80·0	145	73	145	87‡	100	S. I. F_4
3	17.vi.34		65	1	1	37	39	1	1	182·0	56·0	182	56	182	56	100	S. I. F_3
29	7.xi.34		75	2	4	31	59	6	1·50	52·0	81·0	47	50	57	160	100	F_x†
1	15.v.34		75	4	3	35	41	2	0·66	33·5	40·0	1	2	67	59	90	S. II. F_1
3	20.ix.33		80	3	4	—	—	0	0	272·7	144·5	244	6	306	244‡	100–80	S. I. F_2

* Previous generation reared at varied temperature and humidity.

† F_x progeny of ♂ Stock I. F_3 × ♀ Stock II. F_1.

‡ Females dissected immediately after death, ovaries immature.

§ ,, ,, ,, ,, approximately ¾ developed.

‖ The humidity rose to over 45% at the beginning of the experiment which may account for sexual maturation occurring and only 1 egg-pod being laid.

TABLE 17.

Nomadacris septemfasciata.

Table showing the effect of different temperatures and humidities on sexual maturation, fecundity and length of adult life.

Ref. No.	Date.	Temp. ° F.	Mean R.H., %.	No. of adults. ♂.	No. of adults. ♀.	1st pair *in cop.* Days.	1st egg-pod laid. Days.	No. of egg-pods.	Average no. of egg-pods per ♀.	Length of adult life. Average ♂.	Length of adult life. Average ♀.	Length of adult life. Min. ♂.	Length of adult life. Min. ♀.	Length of adult life. Max. ♂.	Length of adult life. Max. ♀.	Temp. at which hoppers were reared. ° F.	Remarks.
14	10.xi.34	90	30 for 40 days then 75	4	4	—	—	0	0	65·0	77·3	11	29	126	141*	90	F_x †
19	30.x.33	90	45 for 50 days then 70	2	1	—	—	0	0	93·5	141	77	141	110	141*	100–80	S. I. F_2
9	18.iv.33	100 ‡ / 80	65–95	6	8	—	34	not known		—	—	—	—	132	132	100–80	S. I. F_1
10	18.iv.34	100 / 80	30–50 for 70 days then 65–95	10	10	38	63	not known		—	—	—	—	—	—	100–80	S. I. F_1
9	8.x.34	100 ‡ / 90	65–80	7	3	—	—	0	0	147·0	173·0	36	145	186	188§	—	F_x †
9/20	13.x.33		varied	3	5	See text.											F_2

* Females dissected immediately after death, ovaries approximately ¾ developed.
† F_x progeny of ♂ Stock I. F_2 × ♀ Stock II. F_1.
‡ High during the day, low at night.
§ Dissected after death, ovaries almost mature.

in any other experiment, the maximum being only 40 days which is not long enough to allow sexual development to occur. At low relative humidity (40%) the length of life was much longer, the maximum being 260 days. The females, in all experiments where oviposition never occurred, were dissected immediately after death and the state of development of the ovaries examined. In all the specimens at a relative humidity of 70% and over, it was found that the eggs in the ovaries were still immature and white, while those at 40% which lived for 188 to 260 days contained eggs approximately three-quarters developed and cream in colour. This indicates that at 90° F. a definite time is required for the eggs to develop and at the high humidity the insects rarely lived long enough.

A few experiments (Nos. 14 and 19, Table 17) were carried out at 90° F. where it was hoped to stimulate sexual development by keeping the adults for a certain time at a comparatively low humidity and then transfer them to a higher humidity. It may be seen from Table 17 that the attempt was unsuccessful. The last females to die in each experiment (141 days) were dissected and it was found that the ovaries were still immature and white, which suggests that development was very slight, if it took place at all, at either humidity.

At 100° F. sexual maturation occurred in a much shorter time than at 90° F., especially in experiments on individuals which, in previous generations, had been kept under varying conditions. The diapause which normally occurs in nature disappears and oviposition takes place, under the most favourable humidity conditions, in 39 days. Up to the present it has been found impossible to break the diapause in more than two successive generations, but this point will be discussed more fully later (see p. 43). It may be seen from Table 16 that there is a definite optimum range of humidity (45–75%), as in *Locusta* and *Schistocerca*, where sexual development occurs. The failure to reach sexual development at 80% relative humidity is obviously the effect of too high a relative humidity since the same generation at 45% relative humidity reared under the same conditions during the hopper stages oviposited. At 75% two different stocks were tested with approximately the same results. Perhaps the most interesting experiments at 100° F. are the two at 65% relative humidity. In one experiment (No. 3) which was on the first generation (F_1) to be kept at 100° F. the individuals became sexually mature in a very short time, while in the other (No. 30) which was on the second generation (F_2) to be kept at 100° F. the locusts paired but failed to oviposit. This suggests that the absence of a diapause in one generation had lowered the vitality of the next. At the low range of humidities one can only say that 40% relative humidity is still within the range of humidity where sexual development occurs, while 25% prevented sexual maturation. It has been found that 25% is too low to permit of long life if the adults have been subjected to it immediately following emergence. Failure to reproduce is obviously due to the low humidity since, when the adults emerged, they were divided into two lots, one at 25% the other at 75% relative humidity, and, at the latter humidity, reproduction occurred.

Results of experiments at 100° F. during the day and 80° F. at night (Table 17) can only be taken with reservation but, as they are with the F_1 generation, it is necessary to draw attention to the rate of sexual development at different humidities. Both experiments were started on the same date (18.iv.33) with the same stock. No. 9 was kept at a relative humidity of approximately 65% during the day and 95% at night (fluctuation caused by change of temperature). In this experiment oviposition took place after 34 days without any diapause having occurred. Experiment No. 10 was run

at the same temperature but the humidity for the first 70 days alternated from 30% during the day to 50% at night. This definitely reduced the rate of sexual development as oviposition did not occur until the 63rd day, which is almost twice the time required by No. 9. As the humidity of No. 10 was increased to the same as No. 9 seven days after the first egg-pod was deposited no further comparison can be drawn. It should also be observed that pairing in No. 10 occurred a considerable time (25 days) before egg-laying commenced.

VIII. Colour Changes in Adults During Sexual Maturation.

Observations on the colour of adult locusts show that there is a marked difference in the colour of immature and mature individuals of the three species. This change is first observed at the base of the hind-wing, where in *Locusta* and *Schistocerca* a bright yellow develops and in *Nomadacris* a reddish-purple. Externally the males of *Locusta* become bright yellow and the females a dull brown. In *Schistocerca* the pink colour of the young adults gradually disappears and a yellow colour develops in the males and a brownish-yellow in the females. In *Nomadacris* two changes take place, the red markings becoming dull brown, and the lighter markings developing a yellow tinge.

Boldyrev (1929) discussing *Locusta migratoria* L. said that the colour, which develops 5 or 6 hours after the adults emerge, never changes. This is contrary to the other record on this species (Faure 1932) and to the records of Bodenheimer (1929), Telenga (1930), Régnier and Lespes (1930) and Michelmore and Allan (1934). It was found, in all my observations, that the colour change was a definite sign of sexual maturation. This is demonstrated by the following experiments :—(1) *Locusta* (see Table 9) at 100° F. and 70% relative humidity copulated 10 days after emergence of the adults, by which time the yellow colour of the males was beginning to develop, while those kept at 90° F. and 70% relative humidity did not copulate or develop the yellow colour until the 15th day after emergence. The colour change in the females in both experiments developed a few days after copulation and thus corresponded with oviposition. (2) *Locusta* adults which were kept at 90° F. and 35% relative humidity and lived almost the normal period but did not reach sexual maturity, failed to display any colour change. (3) In the case of *Schistocerca* (Table 10) the correlation of colour change with sexual maturity is very striking. In an experiment at 90° F. and 70% relative humidity copulation and development of the yellow colour in the males took place 15 days after emergence of the adults, whereas at 40% relative humidity copulation and development of the yellow colour did not take place until 83 days after the emergency of the adults. As copulation and oviposition continue the development of the yellow colour in the males of both species becomes more marked. In many cases the other markings in *Schistocerca* males almost disappear.

The colour changes in *Nomadacris* described above are in agreement with the findings of Mossop (1933, 1933*a*) and Faure (1935). The latter says :—" The egg-laying red locust is therefore yellowish in colour, with reddish under-wings."

IX. The Effect of Copulation on the Maturation of Females.

The length of time between the emergence of adults and the appearance of first egg-pod seems to be governed by the male to a very large extent. It may be seen from Table 9 that if males and females are of the same age and kept at 100° F. and 75% relative humidity the first egg-pod is laid, on the average,

after 14 days, while if males three to four weeks old are paired with young females the time required by the female in four experiments was slightly less :—

Ref. No.	First copulation.	First egg-mass.
1	3 days	13 days
2	4 days	14 days
3	7 days	13 days
4	6 days	12 days

(Average per female 13 days.)

These figures indicate that spermatic fluid has some stimulating effect on the rate of development of the ovaries, and may account for the large number of females of different ages in a swarm laying eggs at the same time. Pospelov (1934) states that females remain immature if copulation does not occur, even when the temperature is sufficiently high. It will be seen later (p. 35) that unfertilised females do develop but at a slower rate.

X. Length of Adult Life.

(a) *The effect of humidity and temperature on the length of adult life.*

The length of adult life is closely linked with sexual maturation. If extreme conditions of humidity and temperature, which are unfavourable to life in general, are excluded, it may be seen from Tables 8 to 17 that the length of life is shortened with an increase in the rate of sexual maturation, which in turn is regulated by humidity and temperature. Owing to the large variation at the different humidities and temperatures it is not possible to produce curves showing how the length of life varies. In order to realise fully how the length of life is affected, it is necessary to consider the other columns of the tables. Moreover, it is not sufficient to compare the average length of life alone, but in addition the maximum must be considered. This is necessary because the average may be considerably reduced by the death of one or two individuals during the early stages of the experiment.

Under laboratory temperature the length of life of *Locusta* adults is much shorter than that of *Schistocerca*. This is explained by the fact that both are very inactive and do not feed often, but as *Schistocerca* is commonly exposed to unfavourable conditions in nature where a diapause occurs, it is able to survive much longer than *Locusta*. At 80° F. the length of life under optimum humidity is longer than at any other temperature and the maximum for *Locusta* (179 days) and *Schistocerca* (198 days) has been attained at this temperature.

Under unfavourable humidity, where sexual maturation was greatly inhibited *Schistocerca* lived 261 days at 90° F. *Locusta* at low humidity (Table 13), which inhibits sexual maturation, does not live any longer than at the high humidity where sexual maturation occurred. This is due to the fact that the optimum range of humidity for this species is so wide that in order to retard sexual development the humidity has to be so low that it becomes injurious. At 100° F. there does not appear to be any very great difference in the length of life of *Locusta* at humidities ranging from 40% to 80%, while that of *Schistocerca* shows a gradual decrease with a rise in humidity.

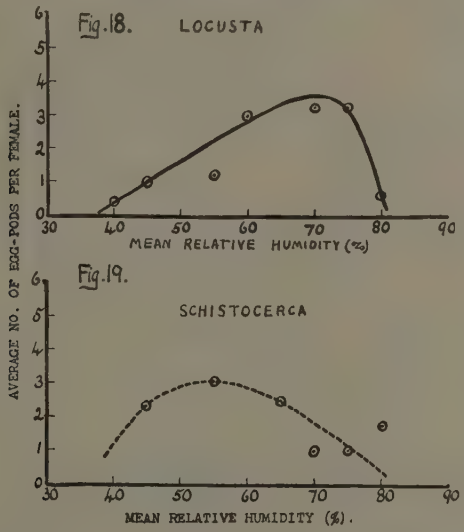
It is very difficult to make any suggestions regarding *Nomadacris*, as the

speeding up of sexual maturation in one generation may have an effect on the next. It should, however, be pointed out that the maximum (306 days) was attained where sexual maturation had not occurred at 100° F. and 80% relative humidity.

(b) *The effect of pairing on the length of adult life.*

The influence of copulation on the length of adult life of *Locusta* is demonstrated by the following experiments in which the males and females were not allowed to pair.

1. Thirty-three males were kept at 90° F. during the day, 80° F. during the night, and at a relative humidity ranging from 65% to 85%. The average length of life was 41·7 days with a minimum of 3 and a maximum of 92 days. This is approximately normal under these conditions.



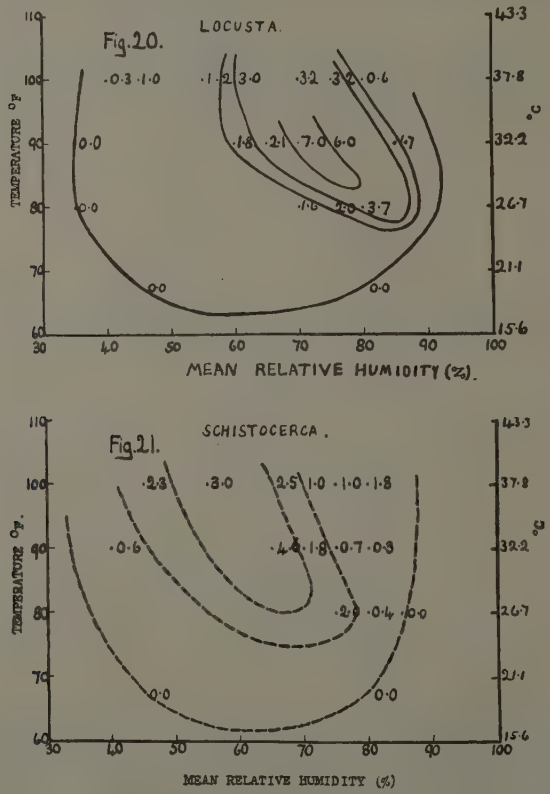
FIGS. 18–19.—The effect of relative humidity at 100° F. on the average number of egg-pods per female: (18) *Locusta migratoria migratorioides*; (19) *Schistocerca gregaria.*

2. In this experiment thirty-four females were kept, for a time, at 90° F. and then at 100° F. and at relative humidity of 75%. The average length of life was 59·9 days with a minimum of 3 and a maximum of 179 days. In all 6 egg-pods were laid by the unfertilised females, but none produced hoppers. The maximum length of life in this experiment far exceeds that where pairing and normal egg-laying occurred under the same conditions, and seems to suggest that it is due to the reduction in sexual development. Pospelov (1934) found also that the length of adult life of females was longer if pairing did not occur, but he states that the ovaries did not develop. In order to investigate this point still further a number of *Locusta* females were killed at different ages and the size of the first egg in each tube was measured. In newly emerged females the average size of the first egg is ·36 to ·42 mm. long and ·12 to ·18 mm. wide. At this stage the eggs are white. When ready for pairing the eggs have increased to between

3·0 and 4·2 mm. long and ·5 to ·9 mm. wide and are cream in colour. Development continues until at the time of, or just before, oviposition they are between 5·1 and 5·4 mm. long and ·9 to 1·2 mm. wide, the colour now being a bright orange-yellow.

XI. The Effect of Humidity and Temperature on Fecundity.

The fecundity of locusts is dependent upon a suitable combination of humidity and temperature. Tables 8 to 11 and 16 and 17 show that at any



Figs. 20–21.—Lines showing equal number of egg-pods per female at different relative humidities and temperatures: (20) *Locusta migratoria migratorioides*; (21) *Schistocerca gregaria*.

temperature between 80° F. and 100° F. there is an optimum humidity where the highest number of egg-pods per female is produced and as the humidity is reduced or increased the number of egg-pods is reduced. At very low humidities (Tables 9, 13, 14 and 16) no eggs are deposited. Owing to lack of sufficient data it is only possible to construct curves of the number of egg-pods laid and relative humidity at 100° F. (figs. 18 and 19). At this temperature there is a

definite optimum humidity range between 65% and 75% for *Locusta* and 50% and 60% for *Schistocerca*. These humidities are slightly lower than what was found to be the optimum for sexual maturation. If humidity and temperature are compared together (figs. 20 and 21), it may be seen, in both species, that with a rise in temperature the optimum relative humidity decreases.

Comparing the effect of humidity and temperature on the number of hoppers, from egg-pods laid by females kept under different humidities and temperatures I found it impossible to observe any difference caused by humidities within the range of 45% to 80%, but temperature had a considerable effect (Table 18). The egg-pods used in these experiments were deposited and incubated in glass tubes each containing sand of approximately the same moisture content. It is only possible to include egg-pods which at least gave rise to some hoppers, as all those which failed to produce any hoppers had to

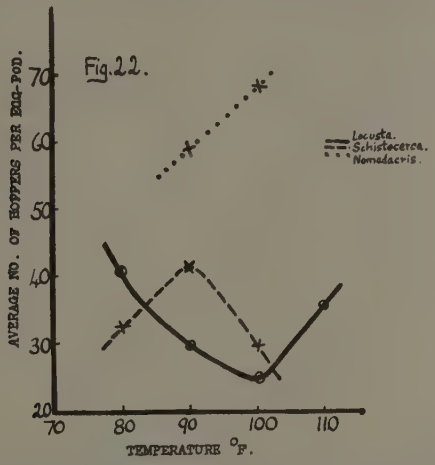


FIG. 22.—The effect of temperature on the average number of hoppers per egg-pod of *Locusta migratoria migratorioides*, *Schistocerca gregaria*, and *Nomadacris septemfasciata*.

be rejected because non-hatching was thought in some cases to be the result of parasitism by a mite. The above results and fig. 22 show that *Locusta* is more fertile at 80° F., and *Schistocerca* at 90° F., while *Nomadacris* gave a higher average at 100° F. than at 90° F. In *Locusta* the average per egg-pod rises again at 110° F. At present it is impossible to say whether this is only accidental and due to the small number of egg-pods or whether it is caused by the locusts producing more eggs at these two temperatures in order to overcome the high mortality during the hopper stages. The first hypothesis is probably the more correct, although the latter cannot be rejected altogether since Rubtzov (1934) has pointed out that the number of eggs produced by individuals of the same species varies according to the habitat. Norris (1933) working on *Ephestia kühniella* found that the average number of " viable " eggs is reduced with the rise in temperature. When considering the above results it is necessary to take into account the effect of temperature on the number of egg-pods per female at optimum humidity. In *Schistocerca* the

average number of egg-pods produced at 90° F. was higher than at any other temperature and as the average number of hoppers produced per egg-pod was also higher it would seem that fecundity is definitely greater at this temperature. *Locusta* gave a higher number of egg-pods at 90° F. than at 80° F. or 100° F. If results at 90° F. and 100° F. are compared this gives a total increase at 90° F. over that at 100° F., but at 80° F. the reduction in the number of egg-pods would tend to counterbalance the increase in the average number of hoppers. *Nomadacris* at 90° F. and 100° F. shows a very similar result to *Locusta* at 90° F. and 100° F.

TABLE 18.

Table showing the effect of temperature on the fecundity of females and on the incubation period of eggs at the optimum humidity.

Temp. ° F.	No. of egg-pods which produced hoppers.	Total no. of hoppers.	No. of hoppers per egg-pod.			Incubation period (days).		
			Average.	Min.	Max.	Average.	Min.	Max.
Locusta migratoria migratorioides.								
80	40	1629	40·8	10	73	23·6	14	32
90	30	858	28·6	2	59	12·6	10	18
100	34	936	24·6	5	69	12·7	9	18
110	6	209	35·8	12	45	10·1	8	11
Schistocerca gregaria.								
80	9	297	33·0	6	59	18·6	16	21
90	26	1090	41·9	6	90	17·1	15	20
100	21	614	29·3	6	56	14·3	12	18
Nomadacris septemfasciata.								
90	2	117	58·5	54	63	25·5	25	26
100	7	471	67·3	44	72	25·7	24	29

XII. EXPERIMENTS ON LOCUST EGGS.

(a) *The effect of temperature on the incubation period.*

Table 18 shows that the incubation period of *Locusta* and *Schistocerca* eggs decreases with a rise in temperature. It should be noticed that in the case of *Locusta* there is practically no difference between the time required at 90° F. and that at 100° F. *Schistocerca* shows a gradual reduction with the rise in temperature. The eggs of *Nomadacris* (Table 18) have only been incubated at 90° F. and 100° F. and it may be seen that the time required is approximately the same at both temperatures.

(b) *The effect of humidity on eggs removed from the sand.*

These experiments were started with consignments of eggs from Africa kept at 90° F. which, as may be seen from Table 18, is a very suitable temperature.

(i) A large number of egg-pods of *Schistocerca* from Morocco were removed from the sand in which they arrived and divided into lots. (*a*) Several hundred egg-pods were placed in tins and covered with moist sand, which should give

100% relative humidity around the eggs. These gave a high percentage hatch. (*b*) About 100 egg-pods were placed in desiccators with water in the bottom. Under these conditions a 100% relative humidity of air should be produced, but the eggs were not in contact with water. None of these eggs hatched; all shrivelled up and rotted.

(ii) Sixty egg-pods of *Nomadacris* from Tanganyika were divided into lots; 20 were covered with moist sand and 40 were placed in desiccators at 100%

TABLE 19.

Schistocerca gregaria.

Table showing the effect of humidity at 90° F. (32·2° C.) on the incubation of eggs removed from the sand at different ages.

Ref. No.	Date.	No. of eggs.	Conditions under which eggs were kept.	Duration of incubation before experiment was started. Days.	No. which hatched.	Average incubation period. Days.	Average under experimental conditions. Days.	% hatch.
1	21.vii.34	10	Controls.	0	8	14·0	14·0	80
2	,,	10	Controls.	0	10	13·8	13·8	100
3	,,	10	Placed on moist sand in closed container.	0	8	13·0	13·0	80
4	,,	10	Placed on zinc in desiccator at 95–100% R.H.	0	0	—	—	0
5	,,	10	Placed on zinc in desiccator at 95–100% R.H.	0	0	—	—	0
6	2.ii.35	10	Controls.	4	8	17·1	13·1	80
7	,,	10	Controls.	4	8	17·6	13·6	80
8	,,	10	Placed on zinc in desiccator at 95–100% R.H.	4	0	—	—	0
9	,,	10	Placed on zinc in desiccator at 95–100% R.H.	4	0	—	—	0
10	,,	10	Placed on cotton-wool in desiccator at 95–100% R.H.	4	0	—	—	0
11	,,	10	Placed on blotting-paper in desiccator at 95–100% R.H.	4	0	—	—	0
12	25.ii.35	10	Controls.	10	8	13·0	3·0	80
13	,,	10	Controls.	10	10	13·5	3·5	100
14	,,	10	Placed on moist sand in closed container.	10	7	14·1	4·1	70
15	,,	10	Placed on zinc in desiccator at 95–100% R.H.	10	10	14·0	4·0	100
16	,,	10	Placed on cotton-wool in desiccator at 95–100% R.H.	10	10	14·0	4·0	100
17	,,	10	Placed on blotting-paper in desiccator at 95–100% R.H.	10	8	14·0	4·0	80

air humidity. The former gave a high percentage of hoppers while all the latter failed to hatch.

As a result of these experiments further work was carried out on eggs kept constantly under known conditions (Table 19). It may be seen from this table that if newly deposited eggs, and those which had completed 4 days of their development under normal conditions in sand, were placed in a relative humidity of 100% they failed to hatch, while eggs which had completed 10 days of their development under normal conditions gave as high a percentage hatch as did the controls. All the eggs were placed on zinc, cotton-wool, or filter-

paper, free from contact with the water in the desiccator. It was also found that if the eggs were placed on moist sand in a relative humidity of 100%, then a high percentage hatch was obtained at all ages of development.

It would appear from these results that it is essential for the eggs in the early stage of their development to be in contact with the particles of water, and that they are unable to absorb the required amount of water from a humid atmosphere. This is very similar to the action of the root-hairs of plants which are only capable of absorbing "capillary water" from the soil. Also, as with plants, locust eggs appear to be unable to carry on respiration in water-logged soil and so rot.

The above results are slightly different from what Bodenheimer (1929) found with experiments on eggs taken in the field at different ages, since he found that eggs which had completed approximately $\frac{1}{3}$ of their development under normal conditions gave a reasonable hatch at 100% relative humidity. He also recorded that a few, which had completed $\frac{1}{3}$ of their development, hatched when kept at a relative humidity of 80%, while in the case of eggs which had completed $\frac{2}{3}$ development the humidity had to be decreased greatly before having much effect on the percentage hatch, and that a few even hatch at 20% relative humidity. In a later paper (1932) he has shown that newly deposited eggs are so sensitive to humidity that it is impossible for hoppers to hatch unless the eggs have been kept under optimum conditions (100% relative humidity in the soil). He also points out that the power to develop at relative humidities below 100% increases with age of eggs.

XIII. Successive Generations Bred with and without a Diapause.

(i) *Locusta* and *Schistocerca*.

Results which may be of some importance as regards the dying down of swarms (especially of *Schistocerca*) were obtained when locusts of these two species were bred for a varying number of generations under optimum humidity conditions at 80° F., 90° F. and 100° F. (Tables 20–25).

In the case of *Locusta* bred at 80° F., it has only been possible to follow the effect on two successive generations. The second generation of this species does not appear to react in any way different from the first. With such a small number of experiments it is impossible to give a final opinion, but as this table is calculated from two series of experiments it is highly probable that had there been any marked difference it would have shown itself.

Continuous breeding of *Schistocerca* at 80° F. has, so far, given a rather indefinite result. The first generation required 114 days to complete the life-cycle under the optimum humidity conditions. Experiments with the second generation were carried out at a relative humidity of 80%, which was rather high. Although oviposition occurred in 46 days, as compared with 59 in the first generation, the eggs were deposited on the floor of the cage and so never hatched, with the result that the second generation did not complete the life-cycle. At this early stage it is impossible to say whether the failure of the females to oviposit in the sand in the tubes was due to the humidity being too high or to a lowered vitality resulting from successive generations at this temperature.

At 90° F. five generations of *Locusta* and four generations of *Schistocerca* were bred within the range of optimum humidity, and except for very slight variations (perhaps due to the small difference in humidity) constant temperature had no apparent retarding effect.

Table 20.

Locusta migratoria migratorioides.

Table showing the time required to become sexually mature and to complete the life-cycle of 2 successive generations at a constant temperature of 80° F. under the optimum humidity.

	F_1.	F_2.	F_3.
Length of hopper life	38 days	39 days	41 days *
Age of adults when first pair seen *in copula*	—	25 ,,	—
Age of adults when first egg-pod was laid	31 ,,	35 ,,	—
Incubation period	27 ,,	20 ,,	—
Total time required to complete the life-cycle	96 days	94 days	—

* Not continued any further.

Table 21.

Locusta migratoria migratorioides.

Table showing the time required to become sexually mature and to complete the life-cycle of 5 successive generations at a constant temperature of 90° F. under the optimum humidity.

	F_1.	F_2.	F_3.	F_4.	F_5.
Length of hopper life	32 days	31 days	28 days	32 days	32 days
Age of adults when first pair seen *in copula*	19 ,,	18 ,,	19 ,,	—	15 ,,
Age of adults when first egg-pod was laid	22 ,,	22 ,,	23 ,,	22 ,,	20 ,,
Incubation period	14 ,,	15 ,,	16 ,,	16 ,,	12 ,,
Total time required to complete the life-cycle	68 days	68 days	67 days	70 days	64 days

Table 22.

Locusta migratoria migratorioides.

Table showing the time required to become sexually mature and to complete the life-cycle of 6 successive generations at a constant temperature of 100° F. under the optimum humidity.

	F_1.	F_2.	F_3.	F_4.	F_5.	F_6.
Length of hopper life	23 days	22 days	22 days	24 days	26 days	24 days
Age of adults when first pair seen *in copula*	14 ,,	17 ,,	15 ,,	14 ,,	17 ,,	10 ,,
Age of adults when first egg-pod was laid	21 ,,	21 ,,	20 ,,	20 ,,	22 ,,	12 ,,
Incubation period	14 ,,	15 ,,	15 ,,	14 ,,	12 ,,	14 ,,
Total time required to complete the life-cycle	58 days	58 days	57 days	58 days	60 days	50 days

TABLE 23.

Schistocerca gregaria.

Table showing the time required to become sexually mature and to complete the life-cycle of 2 successive generations at a constant temperature of 80° F. under the optimum humidity.

	F_1.	F_2.
Length of hopper life	36 days	42 days
Age of adults when first pair seen *in copula* . .	—	—
Age of adults when first egg-pod was laid . .	59 ,,	46 ,,
Incubation period	19 ,,	—
Total time required to complete the life-cycle . .	114 days	—

TABLE 24.

Schistocerca gregaria.

Table showing the time required to become sexually mature and to complete the life-cycle of 4 successive generations at a constant temperature of 90° F. under the optimum humidity.

	F_1.	F_2.	F_3.	F_4.
Length of hopper life	25 days	28 days	25 days	26 days
Age of adults when first pair seen *in copula*	20 ,,	17 ,,	25 ,,	15 ,,
Age of adults when first egg-pod was laid .	22 ,,	22 ,,	29 ,,	19 ,,
Incubation period	18 ,, *	19 ,,	17 ,,	18 ,,
Total time required to complete the life-cycle	65 days	69 days	71 days	63 days

* As these eggs were laid in the sand in the bottom of the cage, this figure is only approximate.

TABLE 25.

Schistocerca gregaria.

Table showing the time required to become sexually mature and to complete the life-cycle of 2 successive generations at 100° F. under optimum humidity. In this experiments two different stocks were tested (see p. 43).

	F_1.	F_2 (Stock I).	F_2 (Stock II).
Length of hopper life	23 days	26 days	25 days
Age of adults when first pair seen *in copula*	—	—	—
Age of adults when first egg-pod was laid.	19 ,,	34 ,,	114 ,, *
Incubation period	13 ,,	16 ,,	—
Total time required to complete the life-cycle	55 days	76 days	—

* These eggs were laid on the floor of the cage and did not hatch.

It is at 100° F. that the important difference occurred. *Locusta* were bred successfully for six generations without effecting development in any way. *Schistocerca*, however, at this temperature appears to be normal during the first generation and reaches sexual maturity slightly sooner than at 90° F., but in the second generation there is a very marked retardation in sexual maturation. Also the length of hopper life was slightly longer during the second than the first generation. Two different stocks of locusts from Africa (1933 and 1934) have been tested. In both cases the adults of the first generation required 19 days to reach sexual maturity, whilst the average time to complete the life-cycle was 55 days. The second generation of the first stock tested became sexually mature and oviposited in 34 days. Some of the eggs hatched but the hoppers all died before reaching the adult stage. The cause of death is partly attributed to lowered vitality and partly to unfavourable humidity conditions. The second generation of stock II behaved even more abnormally. Oviposition did not occur until the 114th day after adults emerged. Only one egg-pod was deposited and this was on the floor of the cage and so never hatched. This not only confirms the results obtained with stock I, but is definite proof that 100° F. is detrimental to sexual maturation. This difference in the results at 90° F. and 100° F. on *Schistocerca* is so striking that one ventures to suggest that conditions, though favourable for the development of one generation, may be harmful to succeeding generations and cause a dying out of the swarm. This hypothesis is put forward in the hope that it may lead to further investigations along this line.

At present it is impossible to say how far it is necessary to raise the temperature before inhibiting sexual development in *Locusta*. In this connection one experiment has been carried out at 110° F. (43·3° C.) and at 70% relative humidity. It was found that the length of hopper life was 20 and 21 days for males and females respectively, which is slightly less than under optimum humidity condition at 100° F. This is what one would expect, but as the percentage of hoppers reaching the adult stage was slightly reduced it shows that the conditions were not optimum. It was, however, during the adult stage that the important difference occurred, since all the males died within three days while the females appeared quite normal. As a result of this other males reared at a lower temperature were added. These lived for several weeks and paired with the females. Oviposition occurred after 25 days when fertile eggs were laid. After making allowance for the males being 3 days younger than the females there is still sufficient evidence to show that sexual maturation was slightly retarded.

Continuing the comparison of the two species a little further under constant conditions, it may be seen that at 80° F. there is very little difference in the time required to complete the life-cycle. Calculating from the data available, there should be approximately five generations of *Locusta* in two years, and four of *Schistocerca*. At 90° F. the rate of development is approximately twice as fast as at 80° F., both species being capable of producing five generations in one year. With a further increase to 100° F. *Locusta* is capable of producing six generations in one year. At this temperature *Schistocerca* completes the first generation in approximately the same time as *Locusta*, but the second generation, as shown above, takes much longer.

(ii) *Nomadacris.*

As this species failed to reach sexual maturity at 80° F. and only succeeded on one occasion at 90° F., it is not possible to follow the effect of successive

generations at these temperatures. It is, however, possible to compare the length of hopper life according to the hoppers hatching from eggs laid and incubated at 90° F. or 100° F. At 70% relative humidity it was found that the average length of hopper life, for progeny of adults kept at 90° F., was 73·0 days for males and 66·5 days for females, while hoppers which were the progeny of adults kept at 100° F. only required 46·4 days for males and 50·5 days for females. This is further supported by an experiment at 75% relative humidity on hoppers hatching from eggs from Mazabuka, Northern Rhodesia. In this case it required, on the average, 51 days for males and 46·3 days for females at 90° F.

At the high temperatures it is possible to break the diapause in the first generation, and probably in the second, by a constant temperature of 100° F. under constant optimum relative humidity, but in order to continue breeding in successive generations without the normal diapause it is apparently necessary to have alternating conditions. It may be seen from Table 26 that four generations were produced in approximately $1\frac{1}{2}$ years. In order fully to explain the results the following general account is given.

TABLE 26.

Nomadacris septemfasciata.

Table showing the time required to become sexually mature and to complete the life-cycle up to the 4th generation.

Temperature :	100°–80° F.	100° F.	Varied.	100° F.	100° F.
Humidity . . .	optimum F_1.	optimum * F_2.	varied F_2.	optimum F_3.	optimum F_4.
Length of hopper life .	43 days	49 days	49 days	41 days	52 days
Age of adults when first pair seen *in copula* .	—	30 ,,	133 ,,	37 ,,	36 ,,
Age of adults when first egg-pod was laid .	34 ,,	38 ,,	135 ,,	39 ,,	—
Incubation period .	30 ,,	—	25 ,,	24 ,,	—
Total time required to complete the life-cycle	107 days	—	209 days	104 days	—

* There are two experiments given for the F_2 generation.

On the 2nd March 1933 hoppers hatched from eggs received two weeks earlier from Africa. These were reared at 100° F. during the day and 80° F. at night under optimum humidity, requiring approximately 43 days to reach the adult stage. When the adults were kept at the same conditions as stated above, it was found that egg-laying commenced on the 34th day after becoming adult,† approximately one-eighth of the time required in nature. The hoppers (F_2 generation) hatched in about 30 days making the time required to complete the life-cycle 107 days. The 30 days required for the incubation of the eggs in this experiment is slightly longer than usual, but may be accounted for by the fact that they were deposited in the sand at the bottom of the cage which never reached the temperature (100° F. and 80° F.) of the air above.

The hoppers of the second generation developed in approximately the average time (49 days) and, as the adults emerged, two experiments were started which will be discussed separately.

† Since writing, the diapause in the F_1 generation has again been broken in two experiments.

(*a*) In this experiment the temperature was 100° F. and the relative humidity 45% until after sexual development took place when the humidity was reduced to 40%. Under these conditions pairing occurred after 30 days and oviposition after 38 days. From this it would appear that the diapause in the second generation could be broken by constant conditions. Unfortunately, only one egg-pod was laid and this failed to hatch, thus bringing this series to an end.

(*b*) The experiment was started on 13.x.33, but, as newly emerged adults were added from time to time up to the end of the 10th day, it is only possible to give approximately the time required for sexual development. The temperature and humidity varied as follows :—At the commencement the temperature was 90° F. and the relative humidity 40%. On the 13th day the humidity was increased to 70% and maintained at this for 24 days, when it was reduced to 45%. After 31 days at these conditions both temperature and humidity were increased to 100° F. and 70% respectively, and maintained at this until the experiment was completed. Thirty-eight days after the temperature and humidity had been increased (*i.e.* 135 days from the commencement of the experiment) copulation occurred and a few days later eggs were found in the sand. The average incubation period for eggs laid was 24 days making the total for the complete life-cycle 209 days, or 316 days for two generations, which is considerably less than one year. This result shows that it is possible to break the diapause in one generation but impossible to do so in the second generation without reducing the vitality. Although a diapause occurred in the second experiment on the F_2 generation, it should be noted that it lasted little more than half the time required in nature.

The third generation which was the progeny of F_2 adults kept under varying conditions, was kept under constant conditions at 100° F. and 65% relative humidity. The time required for sexual maturation (39 days) is very similar to what was found to be the case in the other generations at optimum temperature and humidity, but the eggs laid by this generation, unlike those laid by the F_2 generation at a constant temperature of 100° F., hatched in 25 days. This gives a total of 104 days for the complete life-cycle, which is slightly less than that required by the F_1 generation. The reason for this reduction is due to the longer time required by the eggs of the first generation to hatch, which is, in turn, accounted for by the fact that these eggs were deposited in the sand on the floor of the cage and which were not subject to as high a temperature as those in tubes.

The fourth generation required considerably longer (52 days) to reach the adult stage than either the first (43 days), or the third (41 days), but only slightly longer than the second (49 days). Now, if this is investigated it may be seen that the first generation hatched from eggs from Africa where there had been an adult diapause in the previous generation and that the third generation was the progeny of the second, under varying conditions, which had passed through a diapause, while the second and fourth generations were the progeny of the first and third which had not been subject to a diapause. This suggests that the vitality of the hoppers as well as that of the adults is reduced when the diapause is forcibly broken. The adults of the fourth generation paired on the 36th day, and at this point it appeared that it was going to be possible to break the diapause for the second time in succession. This did not prove to be the case as all the females died without ovipositing. The important point to be noted is that the last female lived for 87 days, which is much longer than the average where the diapause was broken. From these results it

Table 27.

Locusta migratoria migratorioides.

Table showing the rate of development of spermatozoa at different temperatures (° F.) and at optimum relative humidity.

Age (days).	No. of sections per tube.			Distance from base of tube to the highest sperm bundle.								
				No. of sections.			%.			% for all tubes.		
	80°	90°	100°	80°	90°	100°	80°	90°	100°	80°	90°	100°
Just emerged.	148	59	114	—	—	30	—	—	26·3	0	0	26·3
	149	50		—	—		—	—				
	149	44		—	—		—	—				
	150			—			—					
	[illegible]			—			[illegible]					
	[illegible]			—			—					
	95			—			—					
	97			—			—					
	[illegible]			—			—					
3	189	81	125	42	0	75	22·2	0	60·0	24·4	31·8	59·4
	175	80	139	43	23	78	23·9	28·9	56·1			
	201	82	136	49	27	84	24·4	32·9	61·8			
	190	93	134	49	28	78	26·3	30·1	58·1			
		94	132		29	77		30·9	58·3			
		91	141		32	88		35·2	62·4			
			133			78			58·6			
5	72	133	144	26	0	77	36·1	0	53·5	36·7	38·8	56·1
	71	146	142	26	54	73	36·6	37·0	50·7			
	42	150	135	16	57	76	38·1	38·0	56·3			
	70	132	180	30	54	106	42·9	47·8	58·8			
	66		177	21		105	31·8		59·3			
	63			21			33·0					
	66			25			37·8					
10	145	181	182	74	83	115	51·0	45·8	63·2	46·9	50·0	62·1
	144	161	181	77	82	111	53·4	50·9	61·4			
	141	174	147	77	98	92	54·6	56·3	62·6			
	150	163	138	84	85	85	56·0	47·8	61·6			
	105		153	42		100	41·0		65·4			
	105			43			43·0					
	99			40			40·4					
	101			44			43·6					
	94			36			38·3					
	96			37			38·5					
15	197	135	129	106	81	89	53·8	60·0	69·0	54·5	61·7	67·4
	194	139	126	106	91	84	54·6	65·4	66·7			
	202	137	129	111	82	87	55·0	59·8	67·5			
	203	127		111	82		54·7	64·2				
		133			80			60·2				
		140			82			58·6				
		139			86			61·1				
		135			80			63·2				
20	133	126	153	74	80	109	55·6	63·5	71·2	54·5	60·3	71·2
	134	119		72	75		53·7	63·0				
	121	133		71	83		58·7	61·5				
		124			75			61·0				
		119			74			63·0				
		147			84			57·1				
		160			93			58·1				
		151			87			56·7				
25	151	150	160	79	98	124	52·3	65·4	77·5	53·3	65·1	77·5
	142	148		76	96		53·5	64·7				
	139	143		71	93		51·1	65·0				
	138			78			56·5					
	138			71			51·4					
	130			72			54·5					
	123			65			52·8					
30	144		148	100		105	69·5		70·9	64·1		74·2
	168		128	122		93	72·7		71·9			
	166		119	122		95	73·5		79·8			
	176			91			51·7					
	172			95			55·2					
35	258	116		165	82		64·0	70·3		65·7	69·8	
	246	131		166	89		67·4	67·0				
		146			100			68·5				
		154			111			72·1				
60	212			122			57·6			55·0		
	210			115			54·8					
70	191			144			75·3			73·0		
	206			151			73·3					
	228			160			70·2					
	231			170			73·6					

Table 28.

Schistocerca gregaria.

Table showing the rate of development of spermatozoa at different temperatures (° F.) and at optimum relative humidity.

Age (days).	No. of sections per tube.			Distance from base of tube to the highest sperm bundle.								
				No. of sections.			%			% for all tubes.		
	80°	90°	100°	80°	90°	100°	80°	90°	100°	80°	90°	100°
Just emerged.	90		96	—		—	—		—	0		0
	90		97	—		—	—		—			
	96		97	—		—	—		—			
	95		99	—		—	—		—			
			76			—			—			
			72			—			—			
			65			—			—			
3		121	145		74	84		61·1	57·9		59·1	56·8
		123	141		71	82		57·7	58·1			
		119	141		70	75		58·9	53·2			
		112	141		66	80		58·9	56·7			
		119	140		68	81		57·1	57·8			
		121			75			61·9				
5		130	149		72	84		55·4	56·4		54·2	58·1
		126	144		67	85		54·8	59·0			
		124	140		67	79		55·6	60·7			
			140						56·4			
10		141	167		103	106		73·0	63·5		72·5	65·2
		151	167		112	113		74·0	67·6			
		151	168		109	107		72·1	63·7			
		143	167		101	110		71·6	65·9			
15		184	205		134	171		70·9	83·4		74·9	81·0
		171	200		124	154		72·5	77·0			
		175	196		134	161		76·5	82·1			
		166	211		129	167		77·7	79·1			
			214			179			79·0			
20	129	200	175	98	162	129	75·9	81·0	73·7	74·0	80·8	73·6
	132	190	169	100	153	120	75·0	80·5	71·0			
	130		170	97		121	74·6		71·2			
	125		183	89		139	71·2		77·2			
	142		177	103		131	72·5		74·0			
			172			130			75·6			
			179			130			72·6			
25			137			107			78·8			79·0
			163			130			79·7			
30			207			151			72·9			73·8
			193			143			74·1			
			189			141			72·4			
45	165			111			67·3			73·4		
	162			122			75·3					
	158			117			74·1					
	157			116			73·9					
	168			126			75·0					
	163			117			71·7					
	164			119			72·6					
	162			124			76·5					
50	156	214		117	165		75·0	77·1		75·1	75·6	
	151	242		109	190		72·2	78·5				
	151	244		110	185		72·8	74·0				
	143	239		111	180		77·6	75·3				
	147			114			77·6					
	141			107			75·9					
60	180			133			79·4			69·1		
	179			117			65·3					
	173			126			70·3					
	150			97			64·7					
	143			97			67·1					

Fig. 23.

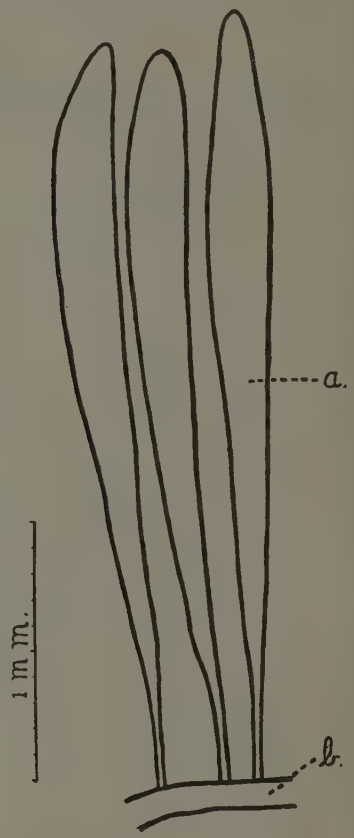


Fig. 24.

Figs. 23–24.—Outline drawing of three follicles and part of seminal duct of male (23) *Locusta migratoria migratorioides*. (*a*) Follicle. (*b*) Seminal duct; (24) *Schistocerca gregaria*. (*a*) Follicle. (*b*) Seminal duct.

would seem that the short diapause which occurred in the second generation was sufficient to revive the vitality of the individuals so that the F_3 generation (Table 26) should really be regarded as an F_1, and F_4 as an F_2. This would indicate that it is necessary for a diapause to occur, at least in alternate generations, which would still allow for two generations in a year.

XIV. The Effect of Humidity and Temperature on the Production of Spermatozoa.

(a) *Hoppers and adults at optimum humidity.*

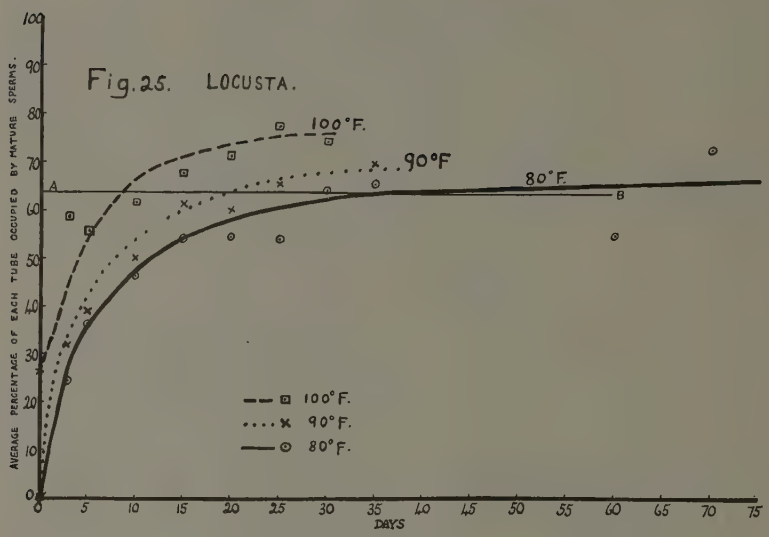
In order to determine the rate of production of spermatozoa at different temperatures (80°, 90° and 100° F.) under optimum humidity conditions, males

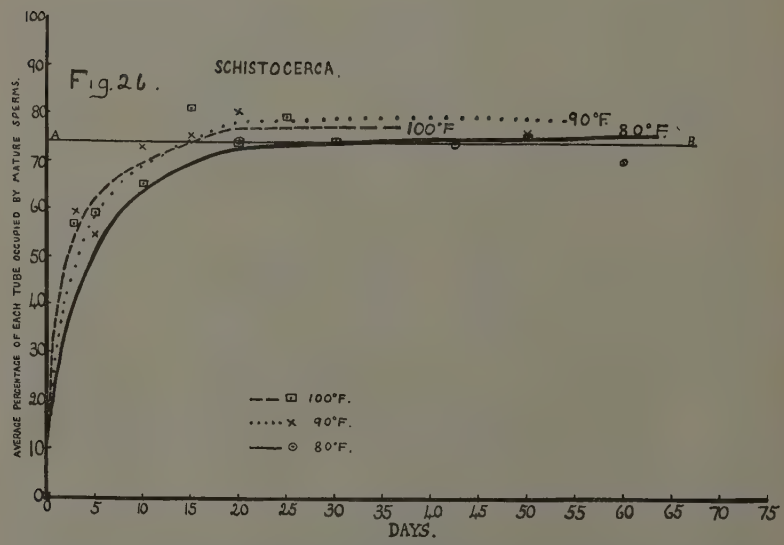
of *Locusta* and *Schistocerca* were kept at the required temperature and prevented from pairing. The males were kept at the same temperature as that at which the hoppers were reared. This was found to be necessary, since the temperature at which the hoppers are reared has a considerable effect on the state of development of the sexual products at the time of emergence of the adults (see below). The insects were killed at different ages and the testes removed, fixed in bouin and sectioned (pl. 2). Owing to the shape and arrangement of the tubes of the testes it was impossible to cut serial sections of the entire organs, so groups of three to five tubes were removed from the centre (figs. 23 and 24) and cut transversely from the free end of the tube to the junction with the seminal duct. The sections were cut 15μ in thickness and stained, first in an aqueous solution of 1% crystal violet, and then in a solution of $\frac{1}{2}$% iodine + $\frac{1}{2}$% potassium iodine in 80% alcohol.

The total number of transverse sections in each tube was counted and the distance from the base of the tube to the highest sperm bundle determined. From this data the percentage of each tube occupied by mature sperm bundles is calculated, together with the average of all the tubes at different ages (Tables 27 and 28). Percentages calculated in this manner are not absolutely correct, since the narrow neck at the base of the tube where no developing cells occur, is also included in the sections. This accounts for the rather sudden rise from 0% to over 25% and 50% for *Locusta* and *Schistocerca* respectively, *Schistocerca* having a longer neck to the tube than *Locusta*. It should also be noted that the maximum length of the tube occupied by mature sperm bundles seldom exceeds 75% of the entire length for *Locusta* and 80% for *Schistocerca*. This is due to the fact that there is always a part at the distal end of the tube occupied by primordial germ cells.

Fig. 25 shows that the rate of development in *Locusta*, at the beginning, is faster with a rise in temperature, but, after a period, the maximum became approximately the same. Also it should be noticed that at the time of emergence of the adults no mature sperm bundles are present when the hoppers were reared at 80° F. and 90° F., but at 100° F. a considerable number was present (26·3%). This point was further investigated by examining the testes of a fifth-instar hopper reared at 100° F. It was found that 25·4% of the tubes (average of 5 tubes) was occupied by sperm bundles, which shows that a fifth-instar hopper at 100° F. is more mature sexually than newly emerged adults at 80° F. and 90° F. If a line A–B be drawn parallel to the abscissa in fig. 25 from the point 64% on the ordinates, it cuts the curves 100° F., 90° F. and 80° F. at 9, 19 and 32 days respectively. This corresponds very closely with the ages at which pairing occurred under optimum humidity at 100° F. and 90° F., but is slightly higher than what was found at 80° F. This would suggest that pairing occurs when a certain proportion of the tubes is occupied with mature sperms.

In the case of *Schistocera* (fig. 26) the effect of temperature is not so marked as in *Locusta*. The points are much more scattered and the curve for 100° F. cuts that for 90° F. This small variation may be due to 90° F. being the optimum temperature, although at 100° F. development proceeds slightly faster for the first few days. In this species mature sperms are never present in the testes when the adults emerge. Further, it is impossible to draw a definite line A–B parallel to the abscissa from a given point on the ordinates, which would cut the curves at the ages corresponding to the times of sexual maturation, but a possible point would be at 74%. This would cut the curves for 100° F. and 90° F. at 15 days and 80° F. at 30 days. This is approximately correct for the first two temperatures, but as pairing was not observed at





FIGS. 25–26.—The effect of temperature at optimum relative humidity on the production of sperm bundles: (25) *Locusta migratoria migratorioides*; (26) *Schistocerca gregaria*.

80° F. it is impossible to draw any comparison. The higher average percentage of each tube occupied by mature sperms in *Schistocerca* (74%) than in *Locusta* (64%) when copulation takes place is due to the difference in the shape of the tubes as illustrated in figs. 23 and 24. The tube in *Locusta* is much broader towards the base than in *Schistocerca* and thus contains the same number of mature sperm bundles in a shorter length of tube.

(b) *Hoppers reared at optimum relative humidity, adults kept at low relative humidity.*

It is proposed to deal with these experiments (Tables 29 and 30) individually.

1. Two male *Locusta* emerged at 90° F. and at optimum relative humidity. They were then transferred to 30% relative humidity. One male was killed after 10 days at this humidity and the other after 12 days, when it was found

TABLE 29.

Locusta migratoria migratorioides.

Table showing the effect of rearing hoppers at optimum relative humidity; the adults on emergence being transferred to a low relative humidity.

Age (days).	No. of sections per tube.	Distance from base of tube to the highest sperm bundle.		
		No. of sections.	%.	% for all tubes.
		90° F. and 30% R.H.		
10	138	68	49·2	
	142	71	50·0	
	143	64	44·7	48·4
	133	66	49·6	
12	153	67	43·8	
	154	79	51·9	47·5
		100° F. and 30% R.H.		
10	180	98	54·4	
	196	101	50·7	52·9

that the average percentage of the tubes occupied with mature sperms was 48·4 and 47·5 respectively. This is just a little below the percentage found under optimum relative humidity.

2. A second experiment was also carried out on *Locusta*, the temperature being 100° F. and the relative humidity reduced to 30% at the time of emergence. In this case the male was killed after 10 days at the low humidity and the percentage occupied by mature sperms was 52·9. According to the curve at 100° F. this is approximately 15% lower than is found under optimum relative humidity and may account for the fact that pairing at this humidity only occurred in one breeding experiment (*cf.* Table 14). Further, it must be pointed out that this percentage is lower than what is found after males have been under optimum humidity for 3 days after becoming adult. This shows that although sperm bundles are present when adults emerge at this temperature under optimum conditions, yet further increase is greatly checked by the reduced humidity.

3. A male of *Schistocerca* from a breeding cage kept at 80° F., which had been transferred to 35% relative humidity on emergence, was removed and killed on the 60th day during which time pairing had not occurred. The average percentage of the tube occupied by mature sperms was 70·6%, which is below the percentage when pairing occurs in *Schistocerca*.

4. At 90° F. *Schistocerca* showed results, when kept at low relative humidity, which coincide with the curves. A male was killed on the 80th day from a

TABLE 30.

Schistocerca gregaria.

Table showing the effect of rearing hoppers at optimum relative humidity; the adults on emergence being transferred to a low relative humidity.

Age (days).	No. of sections per tube.	Distance from base of tube to the highest sperm bundle.		
		No. of sections.	%.	% for all tubes.
		80° F. and 35% R.H.		
60	132	97	73·9	
	132	96	73·2	
	121	85	70·2	
	134	101	75·4	70·6
	134	88	67·4	
	134	90	67·1	
	133	93	69·9	
		90° F. and 40% R.H.		
80	237	179	75·5	
	228	168	73·7	75·4
	222	171	77·0	
		100° F. and 40% R.H.		
40	171	127	74·2	
	161	119	73·8	
	156	119	76·3	73·2
	175	123	63·8	
	176	127	71·1	
		100° F. and 35% R.H.		
60	218	171	78·4	
	218	169	77·5	
	218	169	77·5	76·5
	219	159	72·6	

cage at a relative humidity of 40%. On examination it was found that 75·6% of the tubes was occupied by mature sperm bundles, which indicates that it was approximately at the stage when pairing should occur. This was shown to be correct as the other males left in the cage paired on the 83rd day (*cf.* Table 11).

5. A male *Schistocerca* killed after being 40 days at 100° F. and 40% relative humidity gave the percentage of the tubes occupied by mature sperms as 73·2. This is slightly below the average at optimum humidity and shows that the rate of production of sperm bundles has been reduced.

6. A male *Schistocerca* was kept for 60 days at 35% relative humidity. On

examination it was found that 76·5% of the tubes was occupied by mature sperm bundles. This shows a definite reduction, at this age, but is approximately the stage at which pairing should take place. If compared with the breeding experiments (Table 14) under these conditions, it may be seen that pairing never occurred, which indicates that although the quantity of sperms was approximately high enough for pairing yet they may not be ripe.

(c) *Hoppers reared at unfavourable relative humidity* (45%), *adults kept at optimum relative humidity.*

Only *Locusta* have been tested in this manner (Table 31). It may be seen that this treatment reduced the rate of development very considerably as the percentage of the tubes occupied by mature sperms was 48·2, 60·5 and 64·2 at 3, 25 and 35 days respectively. This is approximately 10% lower than when hoppers and adults were kept at the optimum relative humidity.

TABLE 31.

Locusta migratoria migratorioides.

Table showing the effect of rearing hoppers at 100° F. and at unfavourable relative humidity (45%); the adults on emergence being transferred to optimum relative humidity.

Age (days).	No. of sections per tube.	Distance from base of tube to the highest sperm bundle.		
		No. of sections.	%.	% for all tubes.
3	95	45	47·2	
	100	48	48·0	48·2
	89	44	49·4	
25	166	105	63·2	
	182	108	59·3	60·5
	174	104	59·8	
35	153	104	68·0	
	157	110	70·1	
	154	90	58·4	64·2
	151	91	60·3	

XV. CONCLUSIONS.

The above observations, as far as can be ascertained from the literature, are the only records where the relation of humidity and temperature to the development of the three species under discussion has been studied under controlled conditions. Pospelov (1926) studied the effect of temperature on the rate of development of *Locusta migratoria* L., but he estimated the humidity only approximately, while Boldyrev (1929) in his experiments on the effect of temperature on sexual maturation did not control the humidity. Faure (1932) carried out a few experiments on hoppers of *Locusta migratoria migratorioides*, but as he also failed to control the humidity it is impossible to make any comparison. I am thus unable to compare my results on locusts under controlled conditions with those of other observers, but they must be compared and contrasted with those found under natural conditions, and with what has been found by other observers on different insects.

(a) *Hoppers.*

It has been shown that the rate of development of hoppers is not dependent upon humidity or temperature alone but upon a combination of both factors. The lowest temperature at which complete development takes place is approximately 80° F. (26·7° C.), since hoppers of all species failed to develop beyond the second instar at laboratory temperature (65–70° F.). The highest temperature tested was 100° F. (37·8° C.) for *Schistocerca* and *Nomadacris*, and 110° F. (43·3° C.) for *Locusta*. It was found that, provided the humidity was suitable, the rate of development increased with temperature (*cf.* Pospelov, 1926, who, however, did not control the humidity accurately). I think it likely that 110° F. (43·3° C.) is approaching the upper limit since the percentage of *Locusta* hoppers becoming adult was considerably less than at the lower temperatures. This hypothesis finds support in observations by Janisch (1928), who found that the maximum rate of development is at a temperature very close to that which causes death. In my experiments, however, I have no results to show that there is a decrease in the rate of development near the fatal point.

It may be seen from figs. 5–8 that the optimum relative humidity for the development of *Locusta* is from 50% to 75% and for *Schistocerca* from 50% to 70%. The optimum temperature for *Locusta* is from 90° F. (32·2° C.) approximately, to about 110° F. (43·3° C.). *Schistocerca* has approximately the same lower limit of temperature, but does not appear able to develop at as high a temperature as *Locusta*. The results for *Nomadacris* seem to indicate that the range of relative humidities is approximately the same as for *Locusta*, but the lower limit of temperature appears to be slightly higher.

Below or above the humidities stated the rate of development decreases; the decrease being much greater with a rise in humidity above the optimum range than with a reduction below it. This may be accounted for by the fact that the low humidity which retards development is very close to the humidity which causes death by desiccation. Furthermore, the adverse effect of a low or a high relative humidity is increased with a rise in temperature, and the power to withstand such conditions varies with the species. Hoppers of both *Locusta* and *Schistocerca* are unable to develop at 25% relative humidity at 80° F., but are able to do so at 35% relative humidity. At 90° F. and at 35% relative humidity there is a difference in the two species, *Locusta* being able to develop at that humidity while all the *Schistocerca* hoppers died within a few days. When the temperature is raised to 100° F. neither species is capable of developing at 35% relative humidity. The lowest relative humidity at which development occurred at 100° F. was 45%, and at this humidity a very small percentage of hoppers succeeded in becoming adult. The inhibitory low relative humidity for *Nomadacris* is 30% at 80° F. and 40% at 100° F. In this case humidities nearer the optimum range may also inhibit development, but so far they have not been investigated. Humidities above the optimum show a gradual retardation until the inhibitory high humidity is reached. In the case of *Locusta* the inhibitory relative humidity was found to be approximately 95% at 90° F. and 100° F., while in the case of *Schistocerca* 80% prevented hoppers from becoming adult. At 90° F. *Schistocerca* gave results of interest; with every 5% increase in the relative humidity above 80%, the time the hoppers were able to survive was decreased by 7 days. Hennings (1907, 1907*a*) found also that humidity has a decided inhibiting influence on the development of *Tomicus typographus* L., at the same temperature. Titschak

(1925, 1927), working on the clothes moth, came to the conclusion that low humidity and temperature slightly retarded development, while high humidity and low temperature strongly retarded development, which is in agreement with my results. The data represented by the figs. 5, 6, 7 and 8 are comparable to those of Pierce (1916) and Shelford (1927, 1929), who have made studies of the action of humidity and temperature on the rate of development and have drawn curves showing equal velocity at different humidities and temperatures.

All records of the length of hopper life under natural conditions (Harris 1932, 1933; Ballard, Mistikawi and Zoheiry 1932; Mossop 1933*a*; and Geyer 1934) show that development is generally much slower than under conditions in my experiments. This may be explained by the fact that under natural conditions the hoppers are exposed to intermittent periods of high and low humidity and temperature. Unfortunately, there are no data on the factors inhibiting development under natural conditions.

It is clearly shown in figs. 12 and 13 that the percentage of *Locusta* and *Schistocerca* hoppers becoming adult is dependent on a suitable combination of humidity and temperature. The optimum relative humidity is approximately the same as that at which the maximum rate of development occurred. The most favourable temperature for both species is around 90° F. The optimum for *Nomadacris* also appears to be the same as for the other species. It must be added, as pointed out earlier, that hoppers which have passed the first instar are more able to withstand extreme conditions of humidity and temperature than first-instar hoppers.

(b) *Sexual maturation of adults.*

When comparing the effect of humidity and temperature on the sexual maturation of locusts it is necessary to bear in mind the conditions at which the adults were developing. This is due to the fact that the state of development of the germ cells at the time of emergence of the adults, is affected by the humidity and temperature. As in the case of hopper development it is necessary to have a combination of optimum humidity and temperature in order to obtain the most rapid sexual maturity (figs. 14–17). It is proposed to discuss first the effect of the same humidity and temperature on the adults as that at which the hoppers had been reared and then the effect of low humidities on adults which had developed at optimum humidity. I found that the humidity which inhibited sexual development varied with temperature and species. In the case of *Locusta* a relative humidity of 35% at 80° F. and 90° F. prevented sexual maturation. At 100° F. it was impossible to test this humidity as all the hoppers died, the subsequent relative humidity tested was 40% when it was found that egg-laying occurred after 43 days. These findings are very similar to what Lean (1931*a*) found for *Locusta* under natural conditions. He stated that oviposition never occurs at a relative humidity below 40%. For *Schistocerca* the lowest relative humidity at which sexual maturation occurred was 40% at 90° F. and 45% at 100° F. At relative humidities above the optimum it has been found that sexual maturation occurs in *Locusta* at humidities up to at least 85% at 90° F. At 100° F. experiments have not been conducted at relative humidities above 80%. The period required to reach sexual maturity was much longer than at optimum humidity, and as the average number of egg-pods per female was only 0·66 it is likely that this is approaching the maximum humidity at 100° F. These results agree with the findings of Lean (1931*a*) at the high relative humidities. *Schistocerca* is unable

to become sexually mature at as high relative humidities as *Locusta*, since 80% appears to be the maximum. The optimum range for *Schistocerca* is therefore definitely narrower than in the case of *Locusta*.

Results which are slightly different from those given above were obtained when *Locusta* was reared at optimum relative humidity and transferred to low relative humidity. With such a method it was possible to reduce the relative humidity at which the adults were kept to 25% at 90° F. and for it still to be possible for pairing to occur (Table 13). Furthermore, when the relative humidity was reduced to 30% at 100° F. it was found that pairing and oviposition took place in at least one experiment (Table 14). This provides a striking example of the influence of the conditions under which hoppers developed on the rate of maturation of adults.

Provided the humidity is optimum the rate of sexual development in *Locusta* shows a gradual increase with the rise in temperature from 80°–90°–100° F. In the case of *Schistocerca* there is a marked increase from 80° F. to 90° F. At 100° F., however, sexual development is very little faster during the first generation than at 90° F. In the second generation there is a marked retardation, which shows that 100° F. is detrimental. This would agree with Janisch's (1932) curve, which shows that sterilisation occurs before death.

The exact effect of humidity and temperature on the sexual maturity of *Nomadacris* is still a little obscure. It is, however, possible to point out that the optimum relative humidity is approximately the same as for the other two species, but that the optimum temperature appears to be slightly higher. Up to the present, sexual maturation has never occurred at 80° F., and only on one occasion at 90° F. At 100° F. the rate of sexual maturation appears to depend to a large extent on whether the diapause has been interrupted in the previous generation. If the diapause has not been interrupted in the previous generation, 100° F. and optimum relative humidity are sufficient to cause this and oviposition occurs after 39 to 41 days, while if the diapause has been interrupted in the previous generation oviposition may take place in approximately the time stated above, or death may occur after a period without the insect having become sexually mature.

The effect of humidity and temperature on sexual maturation has also been investigated by sectioning the testes of male locusts kept under different conditions. Figs. 25 and 26 for *Locusta* and *Schistocerca* respectively show that, at the beginning, the production of sperm bundles is faster with a rise in temperature but after a period the maximum becomes approximately the same. Further, it has been demonstrated that in order that pairing may be possible it is necessary for 64% of each testicular tube to be occupied by sperm bundles in *Locusta* and 74% in *Schistocerca*. The seven experiments described above (see p. 51) show that the relative humidity is a very important factor in controlling the quantity of spermatozoa produced.

(c) *Fecundity.*

It has been pointed out that the average number of egg-pods per female at 80° F., 90° F. and 100° F. varies with the humidity. This is clearly shown in figs. 18 and 19, where it may be seen that the optimum relative humidity at 100° F. is between 60% and 75% for *Locusta* and between 50% and 60% for *Schistocerca*. Further, it may be seen (figs. 20 and 21) that with a rise in temperature the optimum relative humidity is gradually reduced. The most suitable temperature for both *Locusta* and *Schistocerca* is 90° F. as the maximum

number of egg-pods (7 for *Locusta* and 4·6 for *Schistocerca*) was laid at this temperature.

In *Nomadacris* the effect of humidity and temperature on fecundity is somewhat uncertain.

(d) *Length of adult life.*

If the extreme conditions of humidity and temperature are excluded it may be seen that the length of adult life is, to a large extent, dependent on sexual maturation, viz. the more rapid the rate of sexual maturity the shorter the length of life. Under optimum relative humidity the maximum for *Locusta* is 179 days at 80° F. and as the temperature is raised to 90° F. and 100° F. there is a gradual diminution in the length of life. In the case of *Schistocerca* the maximum was 198 days at 80° F., but the reduction at 90° F. and 100° F. was not so marked as in *Locusta*. At low humidity where sexual maturity did not occur *Schistocerca* lived for 261 days at 90° F., while *Locusta* lived very little longer at low humidity than at high humidity where sexual maturity was reached. *Schistocerca* at 100° F. showed a gradual reduction in the length of life with a rise in humidity while *Locusta* was very little affected.

Owing to the breaking of the diapause in some generations of *Nomadacris* and not in others, it is very difficult to come to any conclusion for this species.

(e) *Adult diapause.*

The results of the effect of humidity and temperature on the three species of African locusts dealt with show that it is impossible to make a definite rule with regard to the diapause. In the case of *Locusta* there is normally no diapause, except in Northern Rhodesia, and an unlimited number of successive generations may be bred at optimum humidity and at 90° F. and 100° F. If the humidity is low they fail to mature, but there is still no true diapause if the temperature is high, since death occurs at approximately the normal age. For *Schistocerca* it was found possible to rear 4 successive generations at 90° F. and at optimum relative humidity (50–70%) without any marked ill-effects. This shows that although a diapause normally occurs in nature it is not obligatory, and it is possible to break it by a suitable combination of humidity and temperature. It has also been pointed out above, that adults of *Schistocerca* are capable of remaining 113 and 128 days in an immature condition at 90° F. and low relative humidity, and then, with an increase in humidity, to reach sexual maturity. This is almost twice as long as the time required to complete the life-cycle, and shows that a diapause has occurred. *Nomadacris* acts very differently to either of the above species as it is only possible to break the diapause, which normally occurs, and produce viable eggs, in every alternate generation. When, however, the diapause was broken in two successive generations (Table 26), eggs were laid which never hatched or pairing alone occurred but no eggs were laid. Although it is not possible to break completely the diapause in successive generations it is possible to shorten its duration considerably and achieve two complete generations a year, while in nature one is normal.

These results show that Cousin (1932) is not correct in stating that a diapause can be broken if only suitable conditions are obtained. Nor is Roubaud (1933 and 1934) correct in stating that a diapause is always essential in order to re-activate the individuals. It would appear from my work that a diapause is a physiological character depending on the species.

(f) *Specific optimum.*

Finally, the results of the experiments suggest that there is not only a different optimum for the different species, but the different stages, egg, hopper and adult of any one species, have different optima for development which all go to build up the complete cycle. Thus, it is impossible to give definite optimal conditions which will be suitable for all stages of one species. The optimal condition for the species is, therefore, a succession of combinations of factors which are the most suitable for all its stages. Similar conclusions have been drawn by Maclagan (1932) from his work on *Smynthurus viridis* L.

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Explanation of Plates.

Plate 1.

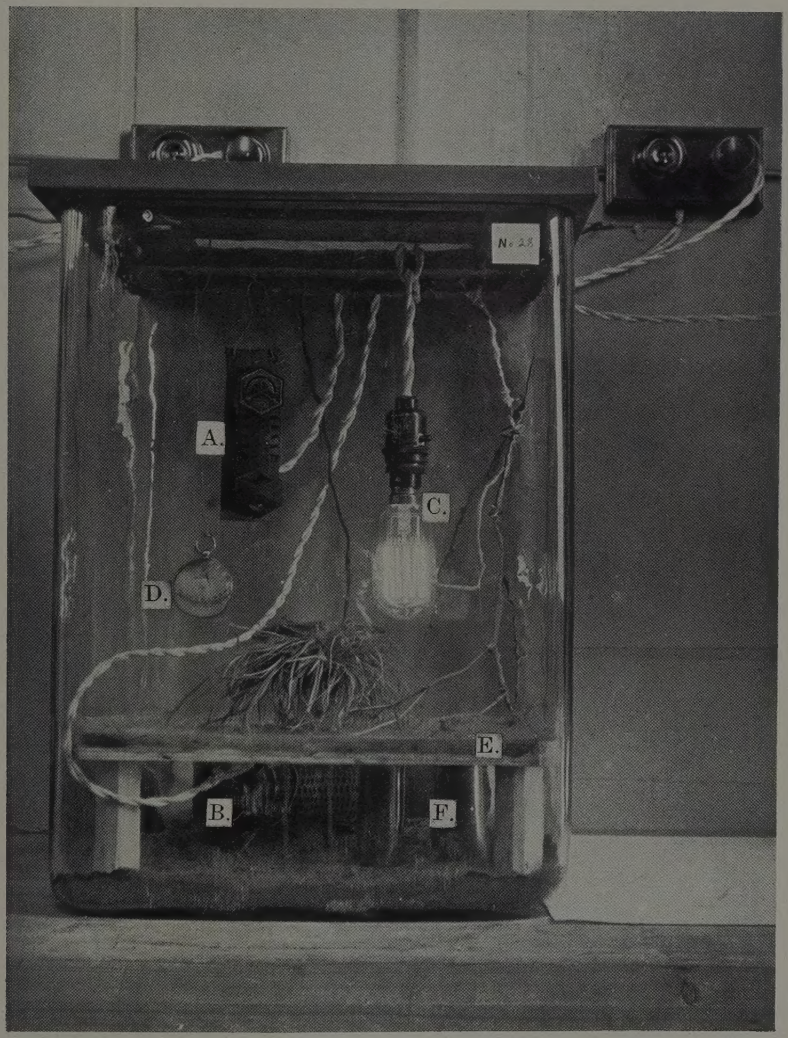
Experimental cage.

A. Thermostat.
B. Heater.
C. Electric Bulb (for lighting only).
D. Hygrometer.
E. Perforated zinc floor.
F. Tubes filled with sand for oviposition.

Plate 2.

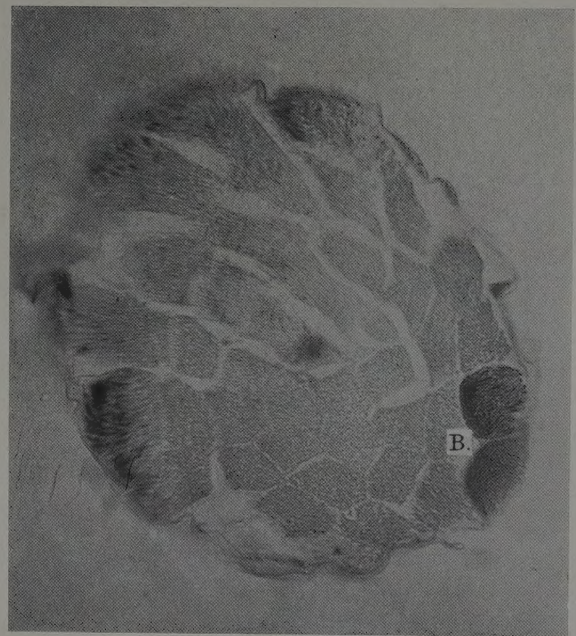
Fig. 1. Longitudinal section of part of a follicle of *Locusta migratoria migratorioides*.
2. Transverse section of a follicle of *Locusta migratoria migratorioides*.

(A. Developing cells. B. Mature spermatozoa.)



The Breeding Cage.

1



2

Sections of follicles of *Locusta*.